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Prefledging survival and reproductive strategies in black brant

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PREFLEDGING SURVIVAL AND REPRODUCTIVE STRATEGIES IN BLACK BRANT

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PREFLEDGING SURVIVAL AND REPRODUCTIVE

STRATEGIES IN BLACK BRANT

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ABSTRACT

We develop a general model useful for estimating survival of young waterfowl between hatching and fledging. Our model allows for interchange of individuals among broods and relaxes the assumption that individuals within broods have independent survival probabilities. We consider point estimation of survival rates and corresponding variances of the point estimators.

We estimated gosling survival of black brant (Branta bernicla nigricans) during summers of 1987-89 on the Yukon-Kuskokwim Delta, Alaska. Eighty-two percent of females radio-marked at hatch fledged at least 1 gosling (brood success). Survival of goslings within broods was estimated by 3 methods: 1) changes in mean brood size through time, 2) observation of goslings associated with marked adults, and 3) age ratios of brant captured in banding drives. Estimates of survival within successful broods averaged 77% and ranged from 57 to 90%. Combining brood success and survival of young within broods yields estimates of overall gosling survival which averaged 64% and ranged from 77% in 1987 to 52% in 1989.

We analyzed variation in egg size of black brant in relation to clutch size, laying date, female age, year, and position in the laying sequence. Egg size increased with clutch size and female age, and decreased with laying date, year, and position in the laying sequence. We did not detect a negative phenotypic correlation between clutch size and egg size. However, overlap in total clutch volumes for clutches of different sizes indicated trade offs occurred among individuals with comparable investments in their clutches.

We web-tagged black brant goslings at hatch, recorded their egg size, position in the egg-laying sequence, initial brood size, hatch date, and nesting density, and examined the effect of these characteristics on their probability of

recapture. Larger broods from larger eggs, and with earlier hatch dates were more likely to be recaptured. There was a tendency for young females to be less successful in rearing their broods; however, this may be related to their egg size, initial brood size, and hatch date, rather than age per se.

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INTRODUCTION

Applied studies on species of interest to wildlife managers frequently have the potential to answer basic ecological questions. My goal in this project was to achieve a balance between addressing management related questions and basic ecology. This study was designed to estimate survival of juvenile black brant. However, in doing this I designed the study to also examine relationships between gosling survival and life history characteristics.

Several methods of estimating the survival of young waterfowl have been used. First, change in the mean number of offspring per brood between hatch and fledging has been used to estimate the proportion of young surviving (McGilvrey 1969, MacInnes et al. 1974, Mickelson 1975, Ball et al. 1975, Zicus 1981, Talent et al. 1983, Hill and Ellis 1984). Second, observation or recapture of individually marked young allow direct estimation of the proportion surviving (Heusmann 1972, Reed 1975). Finally, observations of marked, individually identifiable adults and their broods allows estimation of daily survival rates for young associated with those adults (Ringelman and Longcore 1982, Eberhardt et al. 1989, Orthmeyer and Ball 1990, Savard et al. 1991).

To estimate gosling survival, I used two separate methods of determining the change in the mean number of offspring between hatch and fledging, and used observations of young associated with uniquely marked adults . Thus, I compare and contrast different techniques of estimating of gosling survival. The technique of observing young associated with marked adults to estimate gosling survival requires the assumption that survival of brood mates is independent, and this method is not applicable to populations in which brood mixing occurs (Ringleman and Longcore 1982, Eberhardt et al. 1989). I developed new techniques for estimating juvenile survival that avoid these problems.

Given these estimates of gosling survival, I then examined variation in gosling survival. I hypothesized that the brood rearing success of individual females was not independent of their life-history characteristics. Females hatching large clutches of large eggs early in the season have been shown to fledge, and in some cases recruit, more young (Cole 1979, Findlay and Cooke 1982, Dow and Fredga 1984, Cooke et al. 1984, Rockwell et al 1987, Gauthier 1989). Thus I may be able to predict which young have the greatest survival, and which females have the greatest fitness.

An understanding of the relationships between clutch size, egg size and gosling survival allows examination of optimal allocation of resources to eggs. Clutch size in arctic nesting waterfowl is thought to be limited by stored nutrient reserves (Ankney and MacInnes 1978, Ankney 1984). Additionally, egg size in waterfowl has been shown to be highly repeatable, thus individual females either cannot, or do not, alter their egg size annually (Batt and Prince 1979, Duncan 1987, Lessells et al. 1989). These two relationships lead to the hypothesis that there should be a negative relationship between clutch size and egg size at the population level (Rohwer 1988). That is, if reserves are limited, then phenotypes producing small eggs should, on average, produce more eggs than phenotypes laying large eggs. This prediction assumes that reserves are distributed uniformly across all egg size phenotypes.

If both clutch size and egg size are positively related to fitness, then females producing large clutches of small eggs could have the same fitness as females producing small clutches of large eggs. Many investigators have looked for, but failed to find, a negative relationship between clutch size and egg size (Rohwer 1988, Leblanc 1989, Rohwer and Eisenhauer 1989, Flint and Sedinger 1992). This has been taken as evidence that stored reserves do not limit clutch

size (Rohwer 1988, 1993). However, these studies failed to establish the relationship between clutch size and egg size and fitness.

My goal in this project was to estimate gosling survival to allow estimation of recruitment into the fall flight. To do this I developed survival estimation models that do not require the assumptions of independence in survival among brood mates and no brood mixing. Additionally, I establish the relationship between clutch size, egg size and gosling survival, before looking for a trade off between clutch size and egg size.

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PREFACE

This thesis is written as four separate manuscripts for publication. Each is in the format required for the intended journal. The first two manuscripts have been submitted to the Journal of Wildlife Management. The third manuscript has been published in the Auk 109:896-903. The fourth manuscript will be combined with additional data collected by Dr. Jim Sedinger et al. before submission. Although this is a single authored dissertation, the individual papers are coauthored for publication to acknowledge significant contributions to the papers. The "we" contained in each manuscript refers to the authors listed on the title page for that chapter.

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ESTIMATING PREFLEDGING SURVIVAL: ALLOWING FOR BROOD MIXING AND LACK OF INDEPENDENCE AMONG BROOD MATES

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Abstract: We develop a general model for estimating survival of young waterfowl between hatching and fledging. Our model allows for interchange of individuals among broods, and relaxes the assumption that individuals within broods have independent survival probabilities. The model requires repeated observation of individually identified adults and their offspring, which are not individually identifiable. We show that it is possible to use a modified Kaplan-Meier procedure (Pollock et al. 1989a, 1989b) and a modified Mayfield procedure (Mayfield 1961, 1975; Johnson 1979) under this general modeling framework, and we consider point estimation of survival rates and corresponding variances

of the point estimators. We present a detailed example using data from black brant (Branta bernicla nigricans) broods to illustrate the utility of our procedure when brood mixing occurs and individual fates are not independent.

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Key Words: Brood mixing, estimating survival, Kaplan-Meier, Mayfield, nonindependent survival.

Estimation of survival of young waterfowl between hatching and fledging is a valuable tool in the management of populations. One method of estimating survival of young waterfowl involves repeated observations of offspring associated with identifiable adults. Several studies of waterfowl have used such data in combination with a Mayfield estimator (Mayfield 1961, 1975, Johnson 1979) to calculate daily survival rates (e.g., Ringelman and Longcore 1982, Eberhardt et al. 1989, Orthmeyer and Ball 1990, Savard et al. 1991). The Mayfield method results in estimates of daily mortality rate by dividing the number of mortalities by the exposure days for individuals under observation (Johnson 1979).

Pollock et al. (1989a, 1989b) showed that the Kaplan-Meier procedure, commonly used in medical and engineering applications, could be used to estimate survival of animals. The Kaplan-Meier method estimates survival as the proportion of individuals under observation surviving each observation period (Pollock et al. 1989a). Survival across multiple periods of observation is

the product of the estimates for individual periods.

Neither the current Mayfield nor the Kaplan-Meier estimators account for mixing of young among families, which has been documented in 30 species of waterfowl (Eadie et al. 1988, Larsson and Forslund 1992, Flint and Sedinger 1993). To analyze data that include brood mixing, the estimators must be modified to allow for individuals that change families. Additionally, when brood mixing occurs, not all losses from a given family are due to mortality.

The application of both the Mayfield and Kaplan-Meier models to observations of broods associated with marked adults assumes that the survival of individual young is independent of survival of their brood mates (Johnson 1979, Pollock et al. 1989a, Winterstein 1992). Violation of the assumption of intra-brood independence in survival does not bias the survival estimates from either method, but results in an underestimate of the variance (Ringelman and Longcore 1982, Pollock et al. 1989a).

In this paper we develop a general survival rate estimator and an estimate of its variance for data that include brood mixing. Our estimator is applicable when families, but not necessarily individual young, are identifiable. Additionally, we present a method of estimating the variance in survival rate that does not require the assumption that survival of brood members is independent. We also show that the general estimator can be viewed as either a Kaplan-Meier or a Mayfield type estimator.

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THE GENERAL MODEL

We consider the situation where there are marked adult birds (usually females) monitored with their broods at approximately regular intervals. The following problematic conditions apply and must be addressed by our model.

(i) Disappearances due to adoptions cannot be distinguished from disappearances due to deaths in a brood.

(ii) The fates of individuals within the same brood are not independent of each other.

(iii) Survival changes with age of brood members.

We make the following assumptions in our modeling effort.

(i) Marked females are a random sample of the females in the population.

(ii) The fates of individuals in different broods are independent.

(iii) The expected number of disappearances due to adoption from the average brood equals the expected number of adoptions into the average brood. We assume that if 2 broods meet and the broods mix, then when the 2 broods separate there has been no average net loss or gain of members to either brood. This can be viewed

as symmetry in losses and gains due to mixing.

(iv) Initially, we assume all adult females are observed on the same equally spaced schedule; later we will relax this assumption.

(v) We assume each brood under study can be accurately counted at each observation. This assumption is not strictly necessary if we assume that any errors are random with respect to the true brood sizes.

MODIFIED KAPLAN-MEIER MODEL

First, consider monitoring 1 marked female i and her brood for K observation periods, recording the number of members in the brood ($n_{t,i}$) at each time t (Table 1). We denote the conditional probability of survival for brood i from t to $t+1$ by $S_{t,i}$.

Then consider estimation of any $S_{t,i}$. Using assumption (iii) on symmetry of losses and gains due to mixing:

$$E(n_{t+1,i} | n_{t,i}) = n_{t,i} S_{t,i}. \quad (1)$$

That is, the conditional expectation of brood size for brood i at time $t+1$, given the brood size at time t, is simply the brood size at time t times the conditional survival rate for the period t to $t+1$. Therefore, an unbiased estimate of $S_{t,i}$ is:

$$\hat{S}_{t,i} = \frac{n_{t+1,i}}{n_{t,i}}. \quad (2)$$

Allowing that gains and losses are possible due to mixing of broods, this estimate for an individual brood may be >1. Averaged across broods,

however, it is the correct value (i.e., $E(\hat{S}_{t,i}) = S_{t,i}$).

Now, assuming M_t marked females are under observation at time t, we calculate a weighted average to obtain the estimate $\hat{S}_t$, of the population survival rate, where:

$$\hat{S}_t = \frac{\sum_{i=1}^{M_t} w_i S_{t,i}}{\sum_{i=1}^{M_t} w_i}. \quad (3)$$

Using a weight of $w_i = n_{t,i}$ gives:

$$\hat{S}_i = \frac{\sum_{i=1}^{M_t} n_{t+1,i}}{\sum_{i=1}^{M_t} n_{t,i}}. \quad (4)$$

This is the estimate obtained by thinking of the individual brood member as the sampling unit and ignoring intrabrood dependence in survival probabilities. Recall that the estimate of survival is not biased by a lack of independence in survival among brood mates, however, the estimated variance is biased. Thus estimating the standard error of $\hat{S}_t$ using,

$$SE(\hat{S}_t) = \sqrt{\hat{S}_t(1-\hat{S}_t)/\sum_{i=1}^{M_t} n_{t,i}}, \quad (5)$$

based on the binomial distribution, is inappropriate. Instead we use:

$$SE(\hat{S}_t) = \sqrt{\frac{\sum_{i=1}^{M_t} n_{t,i}^2 (\hat{S}_{t,i} - \hat{S}_t)^2}{M_t \bar{n}_t^2 (M_t - 1)}}, \quad (6)$$

from Cochran (1977:66) where $\bar{n}_t = \frac{\sum_{i=1}^{M_t} n_t}{M_t}$ (i.e., the average brood size at time t). Thus we are estimating proportions in a cluster sample design with individual broods as clusters (i.e. broods are the sample unit).

A Kaplan-Meier type estimator can be developed to calculate a survival function over the entire period of interest not just for one observation period. The survival rate up to time t, $[S(t)]$, is estimated as the product of the individual period estimates j up to that time:

$$\hat{S}(t)=\hat{S}_1 \cdots \hat{S}_t=\prod_{j=1}^{t} \hat{S}_j. \qquad (7)$$

The advantages of this approach are:

(i) The variance of the estimates of survival reflects the losses and gains due to brood mixing.

(ii) The variance also reflects measurement errors due to possible difficulties in counting broods.

(iii) The variance estimator avoids possible bias due to inter-dependence of fates of brood members.

(iv) No assumptions have been made about the probability distribution of the $n_{t,i}$'s so that the variances of the estimates are distribution free.

(v) If a marked adult is not relocated it is ignored from that time on.

The disadvantages of this approach are:

(i) There are more parameters than for the Mayfield method, which assumes $S_t = S$. Therefore, we present a modified Mayfield procedure in the next section.

(ii) It is often impossible to observe every brood on the same regular schedule. This can be addressed either by using the modified Mayfield procedure (see next section) or by estimating missing values by assuming constant survival over the observation period.

MODIFIED MAYFIELD MODEL

The key development from the previous section is that we need to calculate the survival rate (using the Mayfield method) separately for each brood. For each brood the estimated probability of daily survival is the proportion of total exposure days that are survived by individuals in the brood. As with the Kaplan-Meier method we assume that we are just as likely to observe increases and decreases in brood size due to brood mixing (assumption iii).

Consider brood $\underline{i}$, where the brood is monitored daily, the Mayfield type estimate of the daily survival rate for brood $\underline{i}$ from $\underline{t}=1$ to $\underline{K}$ is:

$$\underline{\hat{DSR}}_i = \frac{\underline{n}_2 + \cdots + \underline{n}_k}{\underline{n}_1 + \cdots + \underline{n}_{k-1}}, \qquad (8)$$

because $(\underline{n}_2 + \ldots + \underline{n}_k)$ is the total exposure days survived and $(\underline{n}_1 + \ldots + \underline{n}_{k-1})$ is the total exposure days. In practice, some broods will not be observed daily but the usual rules for calculating exposure days apply (Johnson 1979,

Bart and Robson 1982). Calculating exposure days for observation intervals longer than 1 day can be done several ways. First, assume that any change (increase or decrease) in brood size occurred at a given point in the interval (e.g., Mayfield's midpoint assumption; Johnson 1979). Thus both an adoption and a disappearance would be assigned exposure days equal to one half of the observation interval. In this case the daily survival rate for brood $\underline{i}$ is estimated as:

$$\underline{\hat{DSR}}_i = 1 - \left[\frac{\Delta \ \underline{\text{Brood Size}}_{(i)}}{\underline{\text{Exposure Days}}_{(i)}} \right].$$

Where Δ Brood Size is the change (either positive or negative) in the number of goslings associated with brood $\underline{i}$ from the first to the last observation.

Alternative models with no assumptions about the time of change in brood size can be used; however, these models are somewhat more complex. First, following the constraint of the Kaplan-Meier model, where all adult females are observed on the same equally spaced interval, the estimated survival is:

$$\underline{\hat{DSR}}_i = \left[\frac{\underline{n}_{2,i} + \ldots + \underline{n}_{K,i}}{\underline{n}_{1,i} + \ldots + \underline{n}_{K-1,i}} \right]^{1/\underline{L}}, \qquad (9)$$

where $\underline{L}$ is the interval length (i.e., $\underline{t}$ to $\underline{t}+1$) in days (Bart and Robson 1982). Alternatively, if observation interval lengths vary, then the estimate of $\underline{\hat{S}}_i$ must be solved iteratively following Bart and Robson (1982:1080). Given these estimates of survival for each brood, the number of exposure days for each brood can be calculated as:

$$\underline{\text{Exposure Days}}_{(i)} = \frac{\underline{n}_{1,i} - \underline{n}_{K-1,i}}{1-\hat{\underline{S}}_i} = \frac{\Delta\ \underline{\text{Brood Size}}_{(i)}}{1-\hat{\underline{S}}_i}. \qquad (10)$$

Again, we estimate $\hat{\underline{S}}_t$ by taking a weighted average of the $\hat{\underline{S}}_i$ using equation (3) and $\underline{w}_i = \underline{\text{Exposure days}}_{(i)}$, giving:

$$\hat{\underline{DSR}}_t = 1 - \left[\frac{\sum_{i=1}^{M_t} \Delta\ \underline{\text{Brood Size}}_{(i)}}{\sum_{i=1}^{M_t} \underline{\text{Exposure Days}}_{(i)}} \right]. \qquad (11)$$

As with the Kaplan-Meier method, this is the same estimate obtained by ignoring intrabrood correlation. However, the appropriate variance with intrabrood correlation is calculated from equation (6) where

$\bar{\underline{n}}_t = \dfrac{\sum_{i=1}^{M_t} \underline{\text{Exposure Days}}_{(i)}}{\underline{M}_t}$ (i.e., average number of exposure days per brood).

The advantages of this Mayfield model compared to the Kaplan-Meier model are:

(i) Fewer parameters in the model.

(ii) The observation schedule can vary within and among broods.

The disadvantages of the Mayfield approach are:

(i) It assumes constant survival within the period over which $\underline{S}_t$ is estimated, thus the variances of the estimates are not distribution free.

(ii) The Mayfield model assumes an underlying likelihood function.

EXAMPLES

Data from observations of broods associated with marked adults consist of the number of young associated with a particular adult and the date of observation. We present 2 examples of such data. The first is a contrived data set constrained so that all broods are observed on the same equally spaced schedule; we apply both estimators to these data. The second example uses the brood sizes of individually marked families of black brant observed on the Yukon Delta National Wildlife Refuge, Alaska during summer 1989; we apply the modified Mayfield approach to this example.

Example 1.

When the observation schedule is constrained so all broods are observed on the same equally spaced schedule (Table 2), we can calculate both the Kaplan-Meier and Mayfield estimates for comparison. Standard errors for the Kaplan-Meier estimates from equation (6) are $SE(\underline{\hat{S}}_1)=0.080410$, $SE(\underline{\hat{S}}_2)=0.0973248$, $SE(\underline{\hat{S}}_3)=0.0614522$. We can also estimate the daily survival rate within each observation period using the Mayfield model. Because all broods were observed on the same schedule the daily survival rate is estimated with equation (9). The quantity inside the brackets of equation (9) is identical to the Kaplan-Meier estimate. The individual Mayfield estimates of daily survival, $\underline{\hat{S}}_{t,i}$, can be calculated by raising the individual Kaplan-Meier estimates of period survival to the inverse of the period length. Thus $\underline{D\hat{S}R}_1=0.8684^{1/10}=0.9860$, $\underline{D\hat{S}R}_2=1.0303^{1/10}=1.0030$, and

$\underline{\hat{DSR}}_3 = 0.9908^{1/10} = 0.9908$. Exposure days for these estimates was calculated using equation (10). The standard error of these estimates was calculated using equation (6) where $\bar{\underline{n}}_t = \frac{\sum_{i=1}^{M_t} \underline{\text{Exposure Days}}_{(i)}}{\underline{M}_t}$. Thus, $SE(\underline{\hat{DSR}}_1) = 9.19996 \times 10^{-3}$, $SE(\underline{\hat{DSR}}_2) = 9.54716 \times 10^{-3}$, $SE(\underline{\hat{DSR}}_3) = 6.70591 \times 10^{-3}$. The Mayfield model allows comparison of survival estimates to determine if they are significantly different (Johnson 1979). Because these estimates are ordered we need only test sequential estimates.

$$\underline{\hat{DSR}}_1 \text{ .vs. } \underline{\hat{DSR}}_2, \quad \underline{Z} = \frac{0.017}{0.0132574} = 1.28,$$

$$\underline{\hat{DSR}}_2 \text{ .vs. } \underline{\hat{DSR}}_3, \quad \underline{Z} = \frac{0.0122}{0.0116657} = 1.04.$$

Because neither of these comparisons is significant ($\underline{P} > 0.1$) the parsimonious model is the combined estimate, $\underline{\hat{DSR}}_t = 0.9931$. The standard error of this estimate is $SE(\underline{\hat{DSR}}_t) = 4.6095 \times 10^{-4}$. The estimated survival over 30 days is 0.8124 with a 95% confidence interval of 0.6142 to 1.0719.

Example 2

Here the observation interval is allowed to vary both among and within individual broods (Table 3). For simplicity, all changes in brood size are assumed to occur at the midpoint of the observation interval. Data in Table 3 are the observed brood sizes of individually marked families of black brant, relative to the peak of hatching on the Yukon Delta NWR during the summer of 1989. Because there are no clear sub-periods, we must assume constant

survival across the period of the study, thus using equation (11) $\underline{\hat{DSR}}_t = 0.9908$. The standard error of this estimate is $SE(\underline{\hat{DSR}}_t) = 6.4230047 \times 10^{-2}$.

DISCUSSION

Assumption of Independence in Survival of Brood Mates

Numerous authors (Ringelman and Longcore 1982, Eberhardt et al. 1989, Rotella and Ratti 1992, Winterstein 1992) have addressed the potential for lack of independence in survival probability among brood mates. Winterstein (1992) developed a method of testing for intrabrood correlation in survival, using the estimated survival on a per brood basis. Savard et al. (1991) calculated survival on a per brood basis using the Mayfield method and Rotella and Ratti (1992) calcuiated Kaplan-Meier estimates of survival on a per brood basis, but both authors combined these individual brood estimates into an unweighted overall estimate. Additionally, Savard et al. (1991) used a weighted Mayfield estimate of survival on a per brood basis but weighted on the number of ducklings per brood and estimated the standard error by jackknifing.

Many factors influencing juvenile survival in waterfowl are more similar within, than among broods. Female age or breeding experience (Gauthier 1989, Forslund and Larsson 1992), hatch date (Dow and Fredga 1984, Flint and Sedinger unpubl.), brood size (MacInnes et al. 1974, Anderson and Eriksson 1982, Leblanc 1987, Rockwell et al. 1987, Winterstein 1992, Flint and Sedinger unpubl.), and egg size (Flint and Sedinger unpubl.) may all influence juvenile survival. These factors cause survival to be correlated among brood mates, yet

these same factors should cause survival among broods to be less correlated.

The models we develop here avoid the assumption that survival of young within broods is independent by using the brood as the sampling unit (Winterstein 1992). Nevertheless, by using a cluster sample design with broods as clusters, we can still estimate survival of juveniles within broods at the population level.

Brood Mixing and the Assumption of Symmetry

Traditional Mayfield and Kaplan-Meier estimators fail to account for mixing of young among families. Consequently, it is unclear in the theory and application of these traditional models how to treat broods that increase in size between observations. This shortfall is apparent in the calculation of both the estimated survival and its variance.

Eadie et al. (1988) reported that post hatch brood mixing is common in 48% of the species in which mixing has been documented. In some waterfowl populations the normal pattern of brood rearing may involve creching (e.g., common eiders Somateria mollissima, Munro and Bedard 1977) or gangbrooding (e.g., canada geese Branta canadensis, Warhurst et al. 1983); thus, brood mixing will have a substantial effect on the estimates of juvenile survival. In other cases brood mixing may be nonexistent or infrequent (Eberhardt et al. 1989) and thus will have an insignificant effect on the estimates of juvenile survival.

In our models, which allow for young to change families, we assume that

decreases and increases in brood size due to brood mixing are equally observable, which is the same as assuming that the observability of broods is independent of the probability of losing or gaining young by adoptions. This assumption is closely tied to the assumption that marked individuals are a random sample of the population. For example, if female age or breeding experience is related to the probability of losing or gaining young by adoption (Eadie et al. 1988), then the marked sample must accurately reflect the age structure of the total population. Additionally, violation of this assumption could be related to the biology of the species studied. For instance, black brant females that lose their entire brood to mortality or adoption may depart the breeding area, or segregate within breeding areas, before undergoing wing molt. Thus, females that lose all their young to adoption would be less likely to be observed, thereby violating the assumption of equal observability and inflating survival estimates.

The effect of violating this assumption of equal observability will depend on which broods, those increasing or decreasing in size due to adoptions, are more observable. Functionally, the Kaplan-Meier and Mayfield models that we developed estimate mortalities as the difference between observed decreases and increases in brood size. Thus if decreases are more observable, survival will be underestimated, whereas if increases are more observable survival will be overestimated. Additionally, in both cases, the variance of the estimates will be underestimated.

Assumption of Unbiased Counting Error

The traditional Mayfield and Kaplan-Meier models, along with the models that we develop here, assume that the number of young in each brood can be accurately counted at each observation point. This assumption, however, is not strictly required in our models if counting errors are unbiased with respect to the true brood size; that is, if we are just as likely to over-count as under-count the number of young in a brood at a given time. In this case of unbiased counting error, survival will be correctly estimated while the estimated variance among the individual estimates of survival will increase as a result of this error. In many studies, however, the secretive behavior of waterfowl broods may result in an under-count of the number of young in a brood because additional young may be concealed. Again the biology of the species may affect this assumption; diving ducks (Aythyini) frequently use open deep-water habitats, whereas dabbling ducks (Anatini) typically use emergent vegetation and wetland edge habitats (Kantrud and Stewart 1977). If a consistent bias in the error associated with counting broods exists, then the estimated survival will be biased in the same direction as the counting error, and the variance will be underestimated. Counting error is typically difficult to measure, and observers are cautioned to record brood sizes carefully to minimize this error, thereby avoiding potential bias and underestimation of variance.

Comparison of Mayfield and Kaplan-Meier Models

When the Mayfield model, without assumptions about the timing of changes

in brood size, is used with a structured sampling design (e.g., Example 1), the similarity between the Mayfield and Kaplan-Meier models is apparent. The Mayfield estimator of daily survival rate is simply a reduction of the Kaplan-Meier estimator of period survival. In a structured sampling design, neither model is numerically superior, as estimates of period survival are identical and confidence intervals are comparable. The advantage of the Kaplan-Meier model is the lack of assumptions about the shape of the survival function within observation periods, resulting in distribution-free variance estimates. The advantages of the Mayfield model result from testing across intervals, which allows development of a parsimonious model and the estimation of a rate, which allows prediction beyond the range of the data, under the assumption of constant survival.

The plasticity of the Mayfield model is useful when the sampling design varies within, and among broods (e.g., Example 2). The Kaplan-Meier model can only be applied to this design by adding assumptions and interpolating the data to create a structured sampling design. This additional assumption of constant survival, while for a shorter period than required for the Mayfield model, eliminates one of the major advantages of the Kaplan-Meier model.

The models developed above are expansions of existing models (Johnson 1979, Pollock et al. 1989a), thus many of the refinements and tests of assumptions described elsewhere (Miller and Johnson 1978, Johnson 1979, Klett and Johnson 1982, Johnson and Shaffer 1990) apply to our models. We

find the conditional probability method described by Klett and Johnson (1982) particularly useful in assessing the constancy of survival under the Mayfield model with an unstructured sampling design (e.g. Example 2). Finally, while the models described here were developed to estimate juvenile survival within broods of waterfowl, these models may also apply to other situations (e.g., our method of variance estimation would apply to estimation of egg survival within nests) and should provide a new and useful technique for wildlife managers.

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Table 1. Model structure and conditional survival rates.

Parameter	Time periods				
Observation periods	1	2	$\underline{t}$	$\underline{t}+1$	$\underline{K}$
No. observed in brood i	$\underline{n}_{1,i}$	$\underline{n}_{2,i}$	$\underline{n}_{t,i}$	$\underline{n}_{t+1,i}$	$\underline{n}_{k,i}$
Conditional survival rates	$\underline{S}_{1,i}$	$\underline{S}_{2,i}$	$\underline{S}_{t,i}$	$\underline{S}_{t+1,i}$	$\underline{S}_{k-1,i}$

Table 2. Brood sizes observed relative to hatch, Kaplan-Meier and Mayfield survival estimates per brood and for the artificial population.

Day of brood rearing				Kaplan-Meier estimates[a]			Mayfield estimates[b]	
00	10	20	30	$\hat{S}_{1,i}$	$\hat{S}_{2,i}$	$\hat{S}_{3,i}$	$\hat{DSR}_{t,i}$	Exp. Days $_i$
4	3	3	3	0.75	1.00	1.00	0.9895	95.24
4	2	3	2	0.50	1.33	0.66	0.9752	80.65
2	2	3	3	1.00	1.33	1.00	1.0134	74.63
4	4	6	6	1.00	1.50	1.00	1.0134	149.25
4	4	3	4	1.00	0.75	1.33	1.0000	110.00
4	2	2	2	0.50	1.00	1.00	0.9716	70.42
5	6	5	4	1.20	0.83	0.80	0.9936	156.25
4	4	3	2	1.00	0.75	0.66	0.9801	100.50
2	2	2	2	1.00	1.00	1.00	1.0000	60.00
5	4	4	3	0.80	1.00	0.75	0.9834	120.48
Overall survival[c]				0.8684	1.0303	0.9118	0.9931	1017.42

[a] Kaplan-Meier estimates of the proportion of goslings surviving each period of observation for each brood.

[b] Mayfield estimates of daily survival rate over all three observation periods.

[c] Weighted average of the estimates for individual broods. Kaplan-Meier estimates weighted on brood size at the start of observation period. Mayfield estimates weighted on the number of gosling exposure days per brood.

Table 3. Black brant brood sizes observed relative to the peak of hatch and Mayfield survival estimates, for a sample of birds from the Tutakoke River colony, Alaska.

Day of brood rearing[a]			
1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7	ΔB.S.$_i$[b]	EXP$_i$[c]	$\hat{DSR}_i$[d]
- - 4 - - - - - - - - - - - 3 3 - 3 3 3 - - 3 3 3 - -	-1	72.0	0.9865
- - - - 4 3 2 - 2 - - - - - - - 2 - - 3 - - 2 2 2 - -	-2	46.0	0.9565
- - 2 2 3 - - - - - - - - - - - - - - - - - - 3 - 4 3	1	72.0	1.0139
4 4 - - - - - - - - - - - - - - - - 5 - 6 6 6 6 6 6 6	2	127.5	1.0157
- 4 - - - - 4 4 4 - - - - 4 - - 4 - - - - - 3 - 4 4 4	0	96.0	1.0000
4 4 - - - - - - - 2 - - - - 2 2 2 2 - - - - - 2 - 2 -	-2	60.0	0.9667
- - - - 5 - 6 6 - - - - - 6 5 - - - 5 5 5 - 6 4 4 4 4	-1	118.0	0.9915
- - - - - - - - - - - - - 4 - - - - - - - - 2 - - 2 2	-2	35.0	0.9429
- 2 2 2 2 - 2 - - - - - - - 2 2 - - - - - - 2 - 2 2 2	0	50.0	1.0000
- - - - 5 - - - - - - - - 4 - - - - - - - - - - - 3 -	-2	82.5	0.9758
Total	-7	759.0	0.9908

[a] Brood size is noted only when actually seen, dashes indicate that the brood was not observed on that day

[b] Net change in brood size between first observation and last.

[c] Exposure days assuming all changes in brood size occurred at the midpoint of the observation interval.

[d] $\hat{S}_i = 1 - \frac{\Delta B.S._i}{EXP_i}$.

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SURVIVAL OF JUVENILE BLACK BRANT DURING BROOD REARING

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Abstract: We estimated survival of black brant (Branta bernicla nigricans) goslings during summers of 1987-89 on the Yukon-Kuskokwim Delta, Alaska, to measure annual variation in survival and to relate nesting success to estimates of recruitment into the fall flight. Eighty two percent of adult females radio-marked at hatch fledged at least 1 gosling (brood success). Survival of goslings within broods was estimated by 3 methods: 1) changes in mean brood size through time, 2) observation of goslings associated with marked adults, and 3) age ratios of brant captured in banding drives. Estimates of survival within successful broods averaged 77% and ranged from 57 to 90%. Combining estimates of brood success and survival of young within broods yields estimates of overall gosling survival which averaged 64% and ranged from 77% in 1987 to 52% in 1989.

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Key words: Alaska, black brant, Branta bernicla nigricans, juvenile survival.

Estimation of survival of young waterfowl between hatching and fledging is a useful tool in the management of populations. Determination of the number of young recruited into the fall flight is useful for interpretation of fall and winter population counts and for understanding the dynamics and age structure of populations.

Several methods of estimating the survival of young waterfowl have been used. First, change in the mean number of offspring per brood between hatch and fledging has been used to estimate the proportion of young surviving (McGilvrey 1969, MacInnes et al. 1974, Mickelson 1975, Ball et al. 1975, Zicus 1981, Talent et al. 1983, Hill and Ellis 1984). Second, observations of marked, individually identifiable adults and their broods allows estimation of daily survival rates for young associated with those adults (Ringelman and Longcore 1982, Eberhardt et al. 1989, Orthmeyer and Ball 1990, Savard et al. 1991). Finally, observation or recapture of individually marked young allow direct estimation of the proportion surviving (Heusmann 1972, Reed 1975).

In this study, estimation of survival is based on both partial brood attrition and total brood loss; this accounts for adults that lost their brood and left the study population during brood rearing. Total brood loss is defined as the loss of all young associated with a parent, whereas partial attrition is the loss of one or more, but not all, young in a brood. This distinction is important because parents that lose their entire brood may depart the study area to molt. If this occurs, estimates of survival based solely on changes in mean brood size or observation of the broods of marked adults underestimate the number of breeding females with zero goslings and thus overestimate gosling survival. Studies employing radio telemetry to determine the proportion of females that lose their entire broods indicate that total brood loss accounts for a significant proportion of juvenile

mortality (Ringelman and Longcore 1982, Talent et al. 1983, Duncan 1986, Eberhardt et al. 1989, Orthmeyer and Ball 1990, Rotella and Ratti 1992).

Here we estimate survival for juvenile black brant between hatching and fledging. We develop and compare estimates based on changes in mean brood size, age ratios from banding drives, and observations of marked adults. We correct these estimates for total brood loss using data from females fitted with radio transmitters.

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STUDY AREA

This study was conducted during the summers of 1987-89 at the black brant colony located at the mouth of the Tutakoke River (61° 15' N, 165° 37' W) on the outer coastal fringe of the Yukon Delta National Wildlife Refuge, Alaska. The Tutakoke River colony has been the site of research on nesting ecology and demography of brant since 1984, providing a population of marked breeding adults at the beginning of this study.

Nesting occurs in wet sedge meadows dominated by Carex ramenskii, several hundred meters inland from the intertidal mudflats of the Bering Sea coast (Fig. 1). After hatching, most broods move off of the colony to the vegetation-

mudflat interface where they feed on short sedges and grasses such as C. subspathacea and Puccinellia phryganodes.

METHODS

Nesting

We located nests by searching 36 randomly located circular plots (50-m radius) every 4th day from the start of nest initiation through the completion of egg laying. Nests were assigned a unique number, and all eggs were labeled with permanent markers. All nests were revisited just before the estimated start of hatching to document egg loss during the incubation period. Nests were revisited every other day during hatching to determine the hatch date and the number of eggs hatched in each nest. Viable eggs began to show activity 12 to 24 hours before pipping, when goslings began calling, tapping, or scratching (P. L. Flint and J. S. Sedinger pers. obs.). The number of hatched eggs in a nest was recorded only when hatching goslings were present and remaining eggs were addled (putrid smell or presence of liquid contents when shaken lightly), or so delayed in hatching that they could not have been successful (e.g. non-vocal eggs when remainder of clutch was completely hatched). Nests known to contain hatching eggs were then avoided for 48 hours to prevent premature departure of adults. After this time, or after the observed departure of the brood, the nest was revisited and the number of unhatched eggs and hatched shell membranes were recorded. Shell membranes of hatched eggs were defined as being detached from the shell and containing feces. Differences between means for nest parameters, within each year, were examined with t-tests.

Brood Observation

Broods leaving the colony and on brood rearing areas were observed from 3 m tall towers fitted with canvas blinds. Broods were observed up to 25 days

after the peak of hatch from 9 different tower locations over 3 years (Fig. 1). Randomly timed counts of the number of adults and goslings in each brood visible in a 360° scan were conducted whenever a tower was occupied by an observer (hereafter referred to as random counts). Brood size was not recorded for those broods in which the observer was uncertain of the total number of goslings. Additionally, counts were recorded during disturbance events (nearby boat or airplane traffic, or predator disturbance) when broods ran out onto exposed mudflats or entered the water. These events allowed accurate counts of large samples of broods where the observer was certain that additional goslings were not concealed by vegetation. We assumed disturbance events occurred at random times. To reduce the interdependence of samples, only the count from each tower with the largest number of broods for each day was used in the analysis.

Adults marked with uniquely encoded 2.5 cm plastic tarsus bands (see next section) also were observed from towers. Band codes were read with 90-100 X spotting scopes and the number of goslings associated with marked adults were recorded.

Banding

Broods were herded into corral traps 26 to 34 days following the peak of hatch in 1987, and 26 to 31 days following peak of hatch in 1988 and 1989. Recaptures of previously banded adults were recorded. Unbanded adults and juveniles were marked with both metal U.S. Fish and Wildlife Service and uniquely encoded plastic tarsus bands. Ratios of total juveniles to adults captured (age ratios) were calculated for each year.

Radio Telemetry

A sample of 16, 26, and 20 females were fitted with backpack radio transmitters in 1987, 1988, and 1989, respectively. In 1987, 36 g transmitters (≈4% of body weight) manufactured by Wildlife Materials, Carbondale, Ill. were mounted using teflon ribbon in a Dwyer loop configuration (Dwyer 1972). In 1988 and 1989, 26 g transmitters (≈3% of body weight) manufactured by AVM Electronics, Livermore, Calif. were mounted using an adjustable integral harness of PVC coated wire (Dwyer design).

To achieve a representative sample of broods, the location and timing of radio application were stratified within the colony to approximate the distribution of nesting locations and hatch dates, as these variables may influence brood rearing success (Flint and Sedinger unpubl.). For example, half the radios were applied to females nesting in the high-density portion of the colony, which contained approximately one half of the nests on the colony. The proportion of radios deployed each day matched the expected distribution of hatch dates, based on nest initiation dates. Predetermined areas were searched on predetermined days and the first nest encountered with 3, 4, or 5 pipping eggs was selected. Females with these clutch sizes were selected because they were the most common, and the small number of radio-transmitters precluded adequate sampling of females over all clutch sizes (e.g., only 4 females with 2 egg clutches across three years would have been radio tagged if radios were applied in proportion to the proportion of clutches containing 2 eggs). Females to be radio-tagged were then trapped on their nests using bow traps (Mickelson 1975). Nests in which all eggs were pipping were selected because females with vocal eggs returned to the nest quickly after disturbance, and the actual number of eggs hatched was known.

Directional fixes from towers to nest locations were obtained after application of radios, but before release of females in 1988 and 1989. Locations of females were determined every 5 min from the time of release until they returned to the nest. Thus, the time of return by females to their nests could be determined. In 1987 the return of females to their nest was determined visually several hours after the release of the female. Thus we could account for females that abandoned their nest as a result of our handling disturbance.

Presence of radio-tagged females was determined by periodic aerial surveys. On the last aerial survey in each year, radio-tagged females were classified as being in a brood flock, a molting flock (i.e., no goslings present), or absent from the study area. Brood success was estimated as the proportion of the radio tagged females remaining in brood flocks in each year. The confidence intervals for the estimates of brood success were based on a binomial distribution (Conover 1980).

Data Analyses

Application of the Mayfield Estimator.--Observation of broods associated with marked adults showed that mixing was a common occurrence (e.g., brood sizes of some marked adults increased between observations). Existing methods of estimating daily survival rate fail to account for brood mixing (Johnson 1979). However, if we assume that we are just as likely to observe increases and decreases in brood size due to adoptions, then a Mayfield-type estimator (Mayfield 1961) can be applied (Flint et al. 1993). We assumed that changes in brood size occurred at the midpoint of the interval between observations. We estimated the daily survival rate of each brood and then estimated the variance in daily survival rates among individual broods, thereby avoiding the assumption that survival was independent among brood mates (Flint et al 1993). We tested for

variation in daily survival rate across days after the peak of hatching using the conditional probability method (Klett and Johnson 1982), in which individual adoptions and disappearances were partitioned across each day of the observation interval. Using these estimates, we summed the mortalities and exposure days for each day, relative to the peak of hatching, and estimated a separate survival rate for each day. The product of these individual daily survival rates provided an unbiased estimate of the proportion of goslings surviving, assuming constant survival within, but not across, observation intervals.

Change-in-Ratio Estimates.--Two additional estimates of the proportion of goslings surviving to fledging were based on estimates of the mean number of offspring per brood late in brood rearing compared to the estimated number hatched. Mean brood size from random counts was calculated from brood sizes observed during counts from all towers >15-days after the peak of hatch. The 15-day threshold was subjectively determined because only random variation in mean brood size was apparent >15 days after the peak of hatch. Variation in brood size >15 days after the peak of hatch was tested with a one-way analysis of variance. Mean brood size in banding drives was calculated by dividing the total number of juveniles captured by the total number of females with brood patches. We estimated proportion surviving (partial brood attrition) by each of these 2 ratio methods as the mean brood size divided by the mean number hatched per nest. We assumed that the mean brood size based on random counts was independent of the number hatched and estimated the standard error for the proportion surviving following Mood et al. (1974:181). The proportion surviving based on random counts was tested across years by comparing the difference in proportion surviving to a standard normal deviate (z-test).

Estimates of Gosling Survival.--Estimates of changes in brood size and period survival estimates based on the daily survival rate were adjusted to account for total brood loss. This was accomplished by multiplying each estimate of partial brood loss by the probability of a radio tagged female remaining on the brood rearing area (brood success). Thus,

corrected survival = proportion surviving * brood success.

Dividing the proportion of females that lost their entire brood by the estimates of corrected survival yielded the estimated proportion of mortality that can be attributed to total brood loss.

RESULTS

Nesting Data

Clutch size late in incubation was consistently higher than the actual number of eggs hatched in all 3 years ($t_{df>347} > 2.97$, $P < 0.0032$) (Table 1). The number of unhatched eggs accounted for most of the difference between clutch size in late incubation and the actual number hatched. Estimates of the number hatched based on shell membranes in the nest bowl was significantly lower than the actual number hatched in all 3 years ($t_{df>371} > 5.10$, $P < 0.0001$) (Table 1).

Brood Observations and Banding Drives

Daily survival rate (not accounting for total brood loss) varied from 0.9965 to 0.9862 across the 3 years of the study (Table 2). The daily survival rate in 1989 was significantly lower than in 1988 ($Z = 1.65$, $P = 0.0494$) but not 1987 ($Z = 0.9142$, $P = 0.18$). Individual estimates of daily survival rate based on the partitioned data set were lower during the first 5 days after the peak of hatch (Fig. 2). Daily survival rate <5 days from peak of hatching was 0.9935, while daily survival rate >5 days from peak was 0.9980 in 1987. Similarly the estimates were 0.9883 and 0.9975 for 1988, and 0.9792 and 0.9877 for 1989. Testing for differences in these

rates was not possible because not all broods were observed on day 5 after peak of hatching, thus the standard error cannot be calculated among broods. Mean brood size observed during random counts increased until 15 days after the peak of hatch ($F_{1,1176}=9.67$, $P=0.002$); however, there was no change in mean brood size between 15 and 25 days after the peak of hatch ($F_{1,1162}=0.2164$, $P=0.642$) (Fig. 3). The calculated mean brood size based on age ratios of flocks captured during banding was lower than that observed during random counts (Table 1).

Radio Telemetry and Gosling Survival

All females ($n=62$), except 1 in 1987, returned to their nests and successfully hatched clutches after being fitted with radio transmitters. The female that failed to return was excluded from further analysis. The proportion of radio-tagged females remaining on the study area in brood flocks (brood success) ranged from 81 to 87% across years (Table 3). Departure of females that lost their entire brood was complete by 20 days after the peak of hatch (Fig. 4). Three of the radios not found on the last flight in 1989 were observed to be non-functional at Izembek Lagoon, Alaska in late October (D. Ward pers. comm.). The brood success of these 3 females could not be determined because the date of radio failure was unknown. We therefore excluded these 3 females from the estimate of brood success for 1989; however, upper and lower bounds for this point estimate of brood success can be determined by assuming all non-functioning radios were associated with brood loss, or conversely, that none were associated with brood loss. Thus the upper and lower bounds for the 1989 estimate of brood success were 70-85%. Accounting for total brood loss, we estimated that between 52 and 77% of goslings survived to fledging in 1987-89 (Table 3). The corrected estimates of survival and the proportion of mortality due to total brood loss declined over the 3 years of the study (Table 3).

DISCUSSION

Nesting Data

Assessment of the actual number of eggs that hatch per nest is important in correctly estimating gosling mortality. Using the observed clutch size immediately prior to hatching overestimates the initial brood size and, thus, causes underestimation of early gosling survival. Unhatched eggs accounted for more than one half of the observed difference between clutch size before hatch and actual number hatched. We likely underestimated the number of unhatched eggs because glaucous gulls (Larus hyperboreus) removed some of these eggs soon after brant abandoned their territories. Estimating the number hatched per nest based on remaining shell membranes underestimated the number of goslings produced, thus causing overestimates of early gosling survival. Therefore, using nesting indices as an estimate of initial brood size should be done with caution. Estimates of total productivity (number of goslings fledged) are insensitive to the difference between egg failure and gosling mortality. However, accurate determination of the number of goslings produced from each nest is important for partitioning the timing of mortality and determining a survival function.

Brood Observations

Gosling survival based on mean brood size observed during random counts yielded the highest estimate of survival of the 3 methods in 2 of 3 years. Mean brood size from random counts, however, may overestimate actual brood size due to observer bias. Adults with no goslings may have been less likely to be recorded in random counts because observers assumed that goslings were present but not visible. Further, small broods may have been excluded from counts because observers believed the count was incomplete. Nevertheless,

these sources of error were not important for counts recorded during disturbance events when all goslings were visible. Another factor that may produce a positive bias in estimated survival from random counts relative to estimates from the other 2 methods is that random count observations were only conducted through the 25th day after the peak of hatch. Banding drives were conducted as late as the 34th day after the peak of hatch and survival estimates based on daily survival rates were calculated for a 40-day fledging period (Bellrose 1976). In comparing these 3 estimates we assumed that no mortality occurred after 25 days from the peak of hatching. Although these data for change in mean brood size (Fig. 3) and daily survival rate (Fig. 2) suggest that little loss occurred after 25 days, failure of this assumption would produce a positive bias in survival estimates from random counts. These biases may explain why our results conflict with those of Savard et al. (1991) who reported that survival estimates based on changes in mean brood size were consistently lower than estimates based on daily survival rate.

Mean brood size increased until approximately 15 days after the peak of hatch then stabilized until observations ended. Warhurst et al. (1983) also observed an increase in brood size after hatch in a population of Canada geese (Branta canadensis) in which brood mixing was frequently observed. The peak in mean brood size (15 days) corresponds with the age at which young geese are thought to recognize their parents (Ramsey 1951). We hypothesize that the increase in mean brood size was caused by the departure of females no longer attending goslings. An increase in mean brood size would occur if entire broods are adopted, followed by the departure of adults no longer attending goslings. The stabilization of brood success (Fig. 4) coincident with the peak in mean brood size (Fig. 3) supports this hypothesis, as most of the radio-tagged females that left the study area did so during the first 15 days after the peak of hatch.

We believe that estimated survival based on observations of broods associated with marked adults, combined with total brood success, provides our most accurate estimate of survival (Table 2). This estimate assumes that daily survival is constant throughout the brood rearing period. Daily survival rate for the first 5 days was lower than for the remainder of brood rearing, however, the significance of this pattern is unknown. If daily survival rate varies with gosling age, the product of the individual daily rates is an unbiased estimate of the proportion surviving (Klett and Johnson 1982). The estimated proportion surviving, allowing for variable daily survival, by this method (Table 2) is within 4% of that calculated under the assumption of constant daily survival. Thus, while daily survival rate increased during the first 5 days after hatching, the effect of non-constant survival on estimated survival to fledging was small.

Banding

Mean brood size from banding drives was potentially under estimated because goslings were less likely than adults to be captured. Goslings may have become separated from adults and hidden in tall vegetation during some drives. Additionally, we may have captured females that failed to successfully hatch a clutch along with brood flocks. Both of these errors would result in an underestimation of mean brood size based on age ratios of birds captured, and thus, an underestimation of survival. Also, broods were captured in several areas that were not sampled from observation towers (Fig. 1); thus the observation of marked adults and random counts may have sampled a slightly different population than the banding drives. However, the effect of this potential error is expected to be random. Survival calculated from the age ratios of birds captured in banding drives was the lowest of the 3 estimates in all 3 years. Although, the survival estimate based on age ratios at banding is probably negatively biased,

the bias appears to be relatively consistent and consequently this estimate may serve as an adequate index of annual prefledging survival (Fig. 5).

Radio Telemetry

The use of radio transmitters to determine brood success assumes that the radios had no effect on the ability of females to rear their broods. Most females returned to the nest in $\leq$20 min (P. L. Flint unpubl. data), and all but 1 successfully hatched at least part of their clutches, suggesting that the initial effect of handling adults was minimal. Additionally, Sedinger et al. (1990) reported no effect on daily energy expenditure of similar size and weight transmitters attached to juvenile black brant in captivity. However, changes in waterfowl behavior have been associated with carrying radio transmitters (Gilmer et al. 1974). Greenwood and Sargeant (1973) detected a decrease in weight of captive mallards and blue-winged teal fitted with radio transmitters compared to control birds. We, however, detected no difference in weight gain between hatch and capture at banding for females fitted with radio transmitters and females tarsus banded at hatch (Flint and Sedinger unpubl.). We infrequently observed females carrying radio transmitters, and although there was no obvious behavioral response to the transmitters we do not know for certain the effect of transmitters on the behavior or brood rearing ability of females. Thus we must assume that the radio transmitters had no effect on our estimates of brood success.

Additionally, the use of radio transmitters to determine brood success assumes that the absence of a radio signal was not due to radio failure. Using the detection of radios at Izembek Lagoon as a check of radio failure accounted for all but 3 females in 1989. We assumed that radio failure was independent of brood success and excluded these 3 females from the point estimate of brood success for 1989.

Published estimates of the proportion of females successfully fledging at least 1 young for other waterfowl range from 0 to 81% (Ball et al. 1975, Ringelman and Longcore 1982, Talent et al. 1983, Duncan 1986, Eberhardt et al. 1989, Orthmeyer and Ball 1990, Rotella and Ratti 1992). Our estimates are near the upper end of this range. Our method of determining brood success classified radio-marked females as being absent from the study area, in a brood flock, or in a failed or non-breeder molting flock. The determination that a female was present in a brood flock does not confirm that the radio-marked individual actually had a brood. This error would positively bias our estimate of brood success. However, our estimates of gosling loss by the other 3 methods accounted for females that lost their brood but remained on the study area in brood flocks. These females were "available" to be observed and captured without goslings (i.e. we included pairs with no goslings in our estimates). Thus, while our brood success estimates may be positively biased, our corrected estimates should account for this potential bias.

Partitioning the loss of goslings into total brood loss and partial brood attrition suggests that a large proportion of gosling mortality is reflected in total brood loss. Brood success only varied 6% across the three years of the study, although, these estimates were based on small samples. The general decline in gosling survival based on estimates of attrition, combined with this constant brood success estimate, caused an overall decline in the estimated proportion of mortality that was due to total brood loss.

Overall, survival across the 3 years studied apparently declined (Fig. 5). We detected a significant decrease in prefledging survival only in 1989, based on our estimates of daily survival, however, our other estimates of survival were associated with large standard errors. There are 2 possible explanations for the

decline in gosling survival across the 3 years studied. The decline in survival could be related to changing age structure of the study population. Nest success was <7% on the Tutakoke River colony in 1984 and 1985 (J. S. Sedinger, unpubl. data). Nesting success increased substantially following removal of Arctic foxes (Alopex lagopus) beginning in 1986 (Anthony et al. 1991). Female black brant tend to show natal philopatry (M. S. Lindberg and J. S. Sedinger, unpubl. data); thus, the proportion of 2- and 3-year-old females in the population should have increased during each year of the study. If brood rearing success is positively related to age or breeding experience (Gauthier 1989, Forslund and Larsson 1992), the observed decline in gosling survival may have been caused by an increase in the proportion of young, inexperienced breeders in the population. The age specific patterns of brood rearing success and molt migration deserve further study. Alternatively, because the breeding population at the Tutakoke River colony increased during the study, the overall decline in survival may be evidence of density-dependent resource limitation.

The overall survival function, a combination of brood success and daily survival rates, suggests that most gosling mortality occurs in the first 10 days of brood rearing. The actual date of departure of unsuccessful females is unknown and data in Fig. 4 should be interpreted as the latest possible date of departure. The precision of this estimate with regard to the timing of total brood loss is restricted by the frequency of aerial surveys and uncertainty about time between brood loss and departure. The apparent pattern of high mortality early in brood rearing has been shown in other waterfowl (Ball et al. 1975, Zicus 1981, Ringelman and Longcore 1982, Hill and Ellis 1984, Mendenhall and Milne 1985, Clark et al. 1987, Savard et al. 1991). This is likely a function of the combined vulnerability to gull predation, intraspecific aggression, and adverse weather

conditions early in brood rearing (Mendenhall and Milne 1985, Owen and Black 1990).

MANAGEMENT AND RESEARCH IMPLICATIONS

Consistent relationships among the 3 different estimates of gosling survival suggests that an index of prefledging survival could be obtained with less effort than we expended in this study. An estimate of mean brood size from counts or banding drives, combined with clutch size data, should provide an adequate index of gosling survival. Mean brood size and brood success were essentially stable >15 days after the peak of hatching, thus brood surveys should be conducted >15 days after hatching.

Further monitoring of gosling survival at the Tutakoke River colony would aid in our understanding of the relationship between population age structure on brood rearing success. If the decline in gosling survival that we observed was related to changes in the age structure of the breeding population, survival should stabilize as the population reaches a stable age distribution. Alternatively, if the decline in gosling survival we observed is related to density dependent resource limitation, we expect survival would continue to decline as long as the breeding population at the Tutakoke colony continues to increase.

The estimates generated herein are useful in predicting fall flights from nesting data. Given estimates of colony size, nesting success, and clutch size, we can now predict recruitment into the fall flight. Additionally, these estimates along with estimates of adult and post-fledging survival are essential in the formulation of an overall population model for black brant.

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Table 1. Clutch size, actual and estimated number of eggs hatched, mean brood size from counts and banding drives, and estimated proportion of juvenile black brant surviving on the Yukon-Kuskokwim Delta, Alaska 1987-89.

Variable	Year					
	1987		1988		1989	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Nesting data						
Clutch size in late incubation[a]	4.10	0.06A[b]	3.92	0.04A	4.16	0.04A
Number of eggs hatched[c]	3.78	0.08B	3.64	0.07B	3.95	0.06B
Estimate of number hatched[e]	3.19	0.07C	2.76	0.06C	3.45	0.06C
Number of unhatched eggs[d]	0.16	0.02	0.15	0.02	0.13	0.01
Mean brood sizes						
Brood size at banding[f]	2.35		1.76		1.63	
Mean brood size from random counts[g]	3.41	0.18	2.80	0.20	2.60	0.22
Uncorrected estimates of partial attrition						
Based on age ratios[h]	62%		48%		41%	
Based on random counts[i]	90%	0.58	77%	0.64	66%	0.59
Based on daily survival rates[j]	87%		82%		57%	

[a] Clutch size on last nest visit prior to visit where hatched or hatching eggs were found.

[b] Mean clutch size compared with number hatched and number hatched compared with estimated number hatched within years using t-tests; means sharing the same letter do not differ.

[c] Number of goslings hatched for nests where goslings were present and remaining eggs were infertile.

[d] Number of unhatched eggs found in nests during visit on hatch date or first post hatch visit.

[e] Number of hatched shell membranes present on first post-hatch visit.

[f] Calculated from adult to gosling ratios of birds captured during banding.

[g] Average brood size observed during random counts >15 days after peak hatching.

[h] Mean brood size at banding / actual number hatched.

[i] Average brood size from random counts / actual number hatched.

[j] Daily survival rate over 40 days from resightings of marked females.

Table 2. Observed changes in brood size of marked adults and estimates of daily survival of Black Brant goslings (uncorrected for total brood loss) on the Yukon-Kuskokwim Delta, Alaska 1987-89.

	Year		
Variable	1987	1988	1989
Observed decreases in brood size[a]	36	78	191
Observed increases in brood size[a]	31	60	84
Estimated number of mortalities[b]	5	18	107
Gosling exposure days[c]	1427	3696	7736
No. of Broods observed	43	84	173
Estimated DSR[d]	0.9965	0.9951	0.9862
Variance[e]	1.18×10^{-4}	2.02×10^{-5}	8.94×10^{-6}
Proportion surviving over 40 days[f]	86.9%	82.2%	57.4%
95% CI[g]	36.6-203%	57.6-117%	45.2-72.7%
Estimate of % survival as a product of individual daily rates[h]	87.4%	80.1%	61.1%

[a] Determined from observations of broods associated with marked adults.

[b] Number of observed decreases minus number of increases.

[c] Number of goslings in a brood times the number of days between observations. Changes in brood size were assumed to have occurred at the midpoint of the observation period.

[d] 1 - (mortalities / exposure days).

[e] Variance among daily survival rates for each brood.

[f] Daily survival rate raised to the power of 40 days, assuming constant survival.

[g] Confidence interval for daily survival rate raised to the power of 40 days, assuming constant survival rate (e).

[h] Product of all individual daily survival rates assuming they are significantly different.

TABLE 3. Brood success and corrected estimates of gosling survival (%) of black brant on the Yukon-Kuskokwim Delta, Alaska 1987-89.

Variable	Year		
	1987	1988	1989
Brood success[a]	86.6	80.8	82.4
95% CI of brood success	60-97	62-93	56-95
Gosling survival from[b] age ratios	53.9	39.1	34.0
Gosling survival from[b] random counts	78.1	62.1	54.2
Gosling survival from[b] daily survival rates	75.3	66.4	47.3
Average survival rate[c]	76.7	64.3	51.7
Proportion of mortality[d] due to total brood loss	57.5	53.8	36.4

[a] Determined from radio tagged females. Radio failure reduces the certainty of this estimate in 1989, potential range 70 to 85%.

[b] Estimate of partial attrition by each method times estimated brood success.

[c] Average of daily survival rate and random count corrected estimates. Age ratio estimate not included in average due to potential bias (see text).

[d] 100% - brood success / 100% - average survival.

Figure Legends

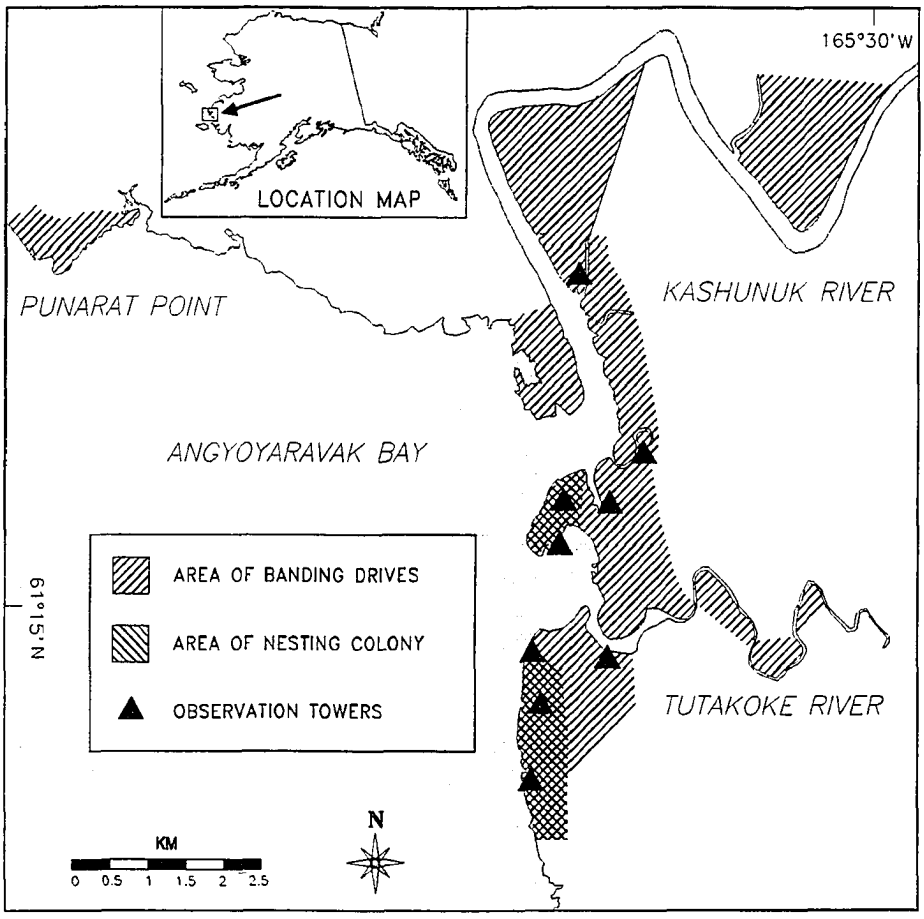
Figure 1. Location of the study area, showing nesting colony, brood rearing areas, and observation tower locations.

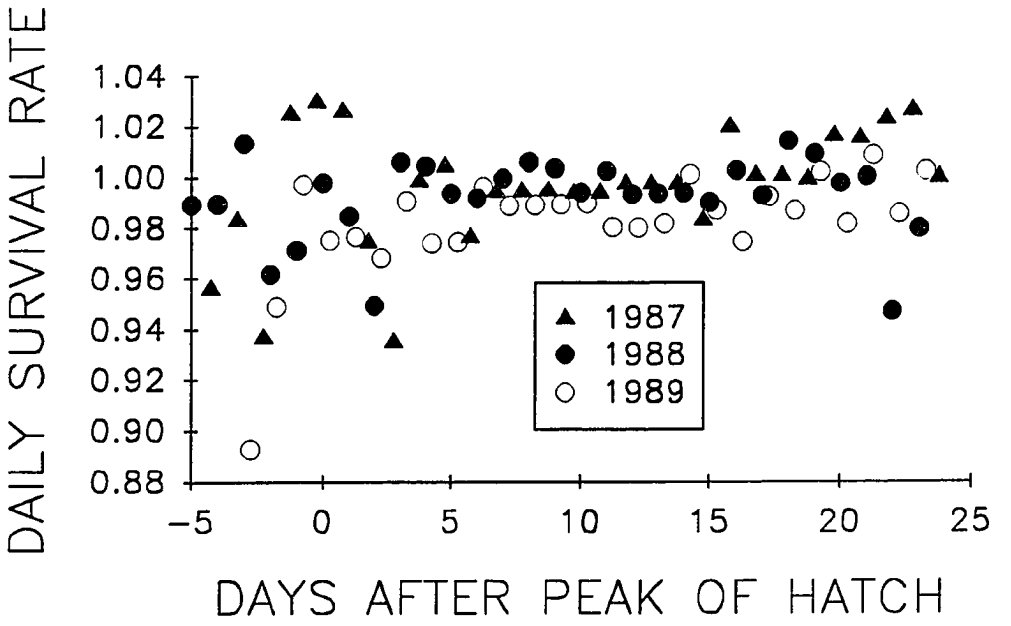
Figure 2. Daily survival rates relative to the peak of hatch of Black Brant goslings calculated by partitioning each disappearance and adoption from broods of marked adults across its observation interval. This partitioning assumes that survival is constant within, but not among observation periods.

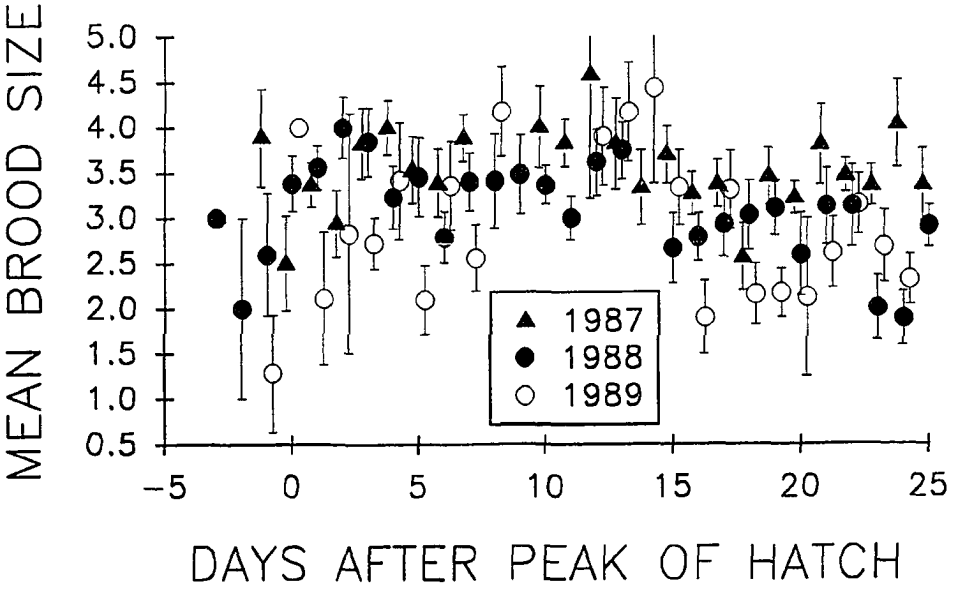
Figure 3. Mean daily brood size from random counts relative to the peak of hatch. Daily mean and the standard error of the mean are presented.

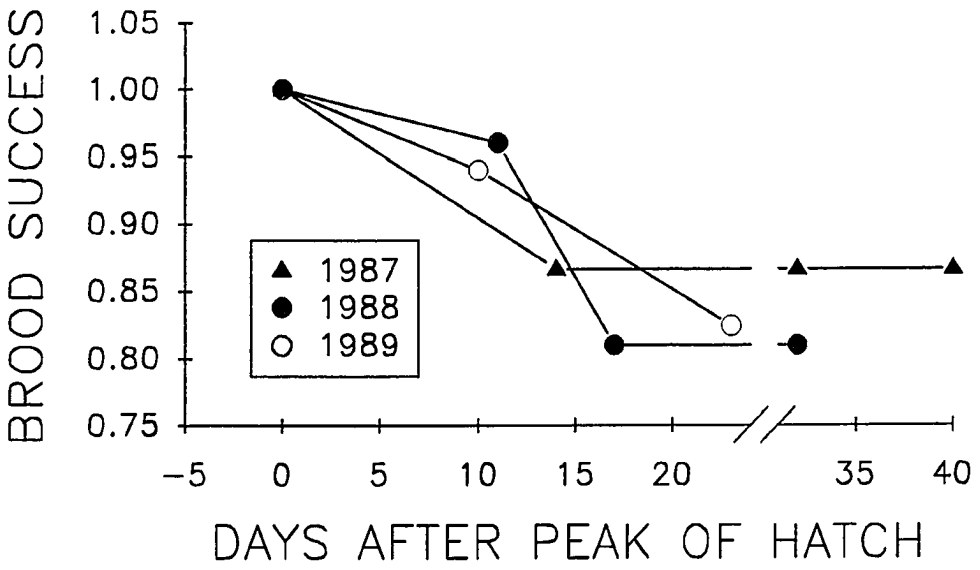
Figure 4. Estimated brood success based on the departure of radio-tagged females relative to the peak of hatch. Resolution is restricted by the frequency of aerial tracking surveys, and points should be interpreted as latest potential date of departure.

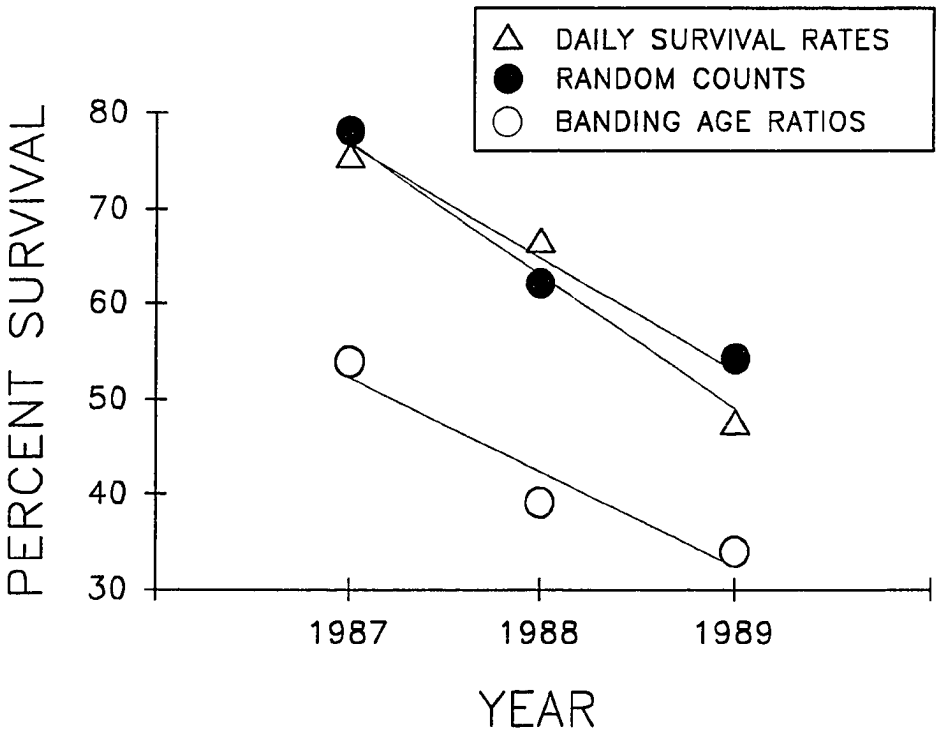
Figure 5. Trends in corrected gosling survival by each of the three methods across the three years studied. Brood success was measured using females fitted with radio transmitters. Proportion surviving within broods was based on daily survival rates of goslings associated with marked adults, changes in mean brood size, and age ratios of birds captured in banding drives.











REPRODUCTIVE IMPLICATIONS OF EGG SIZE VARIATION IN THE BLACK BRANT

RH: Brant egg size variation

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ABSTRACT.- We analyzed variation in egg size of Black Brant (Branta bernicla nigricans) in relation to clutch size, laying date, female age, year, and position in the laying sequence. A total of 3,478 eggs was measured over three years. Egg size increased with clutch size and female age, and decreased with laying date, year, and position in the laying sequence. We did not detect a negative phenotypic correlation between clutch size and egg size. However, overlap in total clutch volumes for clutches of different sizes indicated trade offs occurred among individuals with comparable investments in their clutches. Received 1 October 1991, accepted 30 March 1992.

THE COMBINATION of clutch size and egg size determines the total energetic investment in clutch formation by a laying female. Egg size may affect female fitness through its effects on initial size, early growth and survivorship of hatchlings (Cole 1979, Ankney 1980, Thomas and Brown 1988, Sedinger and Flint 1991), whereas clutch size is related to fitness via its effect on the potential number of offspring produced (Lessells 1986).

Arctic-nesting geese rely heavily on stored lipid and protein reserves for egg production and incubation (Ankney and MacInnes 1978, Raveling 1979, Ankney 1984). Thus, nutrients available for a clutch are limited and at least partially predetermined when geese arrive on the breeding grounds. This limitation on reproductive investment, combined with the fitness advantages of both large clutches and large eggs, creates the potential for both ultimate and proximate trade offs between clutch size and egg size.

Lack (1947) first proposed that trade offs should occur between the number of offspring produced and the size of those offspring. Few examples of such trade offs between clutch size and egg size exist for waterfowl, and possible physiological mechanisms for such trade offs are unknown. The high repeatability of egg size, however, suggests that such trade offs likely occur among, rather than within individuals (Lessells et al. 1989). That is, within the constraints imposed by limited nutrient reserves, individual females do not alter the size of eggs they lay in order to vary their clutch size. Thus, the size of eggs that females produce should influence their average clutch size for those species with constraints on nutrients available for egg production (e.g. arctic-nesting geese). The trade off between clutch size (or number of offspring) and egg size (or size of offspring) is potentially an important component of the life-history characteristics of waterfowl (Rohwer 1988).

Intraspecific variation in egg size has been studied extensively in many species (for review, see Manning 1978). In waterfowl, egg size varies with female age (Cooper 1978, Newell 1988), clutch size (Cooper 1978, Batt and Prince 1979), laying date (Cooper 1978, Hill 1984), year (Cooper 1978, Newell 1988), and position in the laying sequence (Ankney and Bisset 1976, Cooper 1978, Cargill 1979). In general, younger females lay smaller eggs, and egg size declines with laying date and position in the laying sequence.

In this paper we examine relationships between egg size and female age, clutch size, laying date, year, and position in the laying sequence in Black Brant (Branta bernicla nigricans). We interpret these relationships in the context of trade offs between clutch size and egg size.

Methods

Study area.-This study was conducted during the summers of 1987-89 at the Black Brant colony located at the mouth of the Tutakoke River (61° 15' N, 165° 37' W), on the outer coastal fringe of the Yukon Delta National Wildlife Refuge, Alaska. The Tutakoke River colony has been the site of research on nesting ecology and demography of Black Brant since 1984 and, thus, a population of breeding adults marked with uniquely coded plastic tarsus bands existed at the initiation of our study. The Tutakoke River colony covers approximately 12 km^2. Nesting occurs in wet sedge meadows dominated by Carex ramenskii, several hundred meters inland from coastal mudflats. Local nesting density is highly patchy, varying from 0.01 to 280 nests per hectare.

Collection of nesting data and egg measurements.-We located nests by searching randomly located circular plots (radius 50 m) every fourth day from nest initiation through the completion of egg laying. Nests were assigned a unique nest number, and eggs present were assigned a sequence number and marked with permanent markers when they were located. If more than one new egg was present in the nest on a particular visit, laying sequence was established by the degree of shell staining on each egg; first eggs were the most heavily stained (pers. observ.; see also Cooper 1978). We estimated the date of nest initiation by back-dating from the date the nest was located, assuming that one egg was laid per day with a day skipped between eggs 4 and 5 (MacInnes 1962). Maximum lengths and breadths of eggs were measured to the nearest 0.1 mm with dial calipers for all nests located during initiation. We estimated volumes for all measured eggs from the relationship between egg volume and linear measurements (see below). Total volume of the clutch was determined by

summing the individual volumes of all eggs in each clutch. Measurements of eggs for which we were uncertain of the laying sequence were used only in the analysis of total clutch volume. Nests for which an improbable number of eggs were laid between visits (e.g. four eggs in three days), or nests from which eggs marked on a previous visit had disappeared were excluded from all analyses.

We searched the entire colony during incubation to associate marked females with nests. Females were flushed from nests and their tarsus band codes, if present, were recorded. Eggs in nests of marked females were then measured (as described above). Most nests of marked birds were not on plots searched during egg laying. Therefore, initiation dates for these nests were unknown, egg-laying sequence could not be determined, and we were unable to detect either partial predation, and/or nest parasitism.

Repeatabilities.-We estimated repeatability of egg size, clutch size, and clutch volume as the proportion of the total variation in a characteristic (e.g. egg size) resulting from differences among individuals (Falconer 1981, Lessells and Boag 1987). This analysis used data on clutch size from marked individuals nesting in 1984-1986 (J. S. Sedinger unpubl. data) in addition to data collected during this study. Females younger than four years of age were excluded from the repeatability analysis owing to the possibility of age-related variation in egg size or clutch size (see below, Hamann and Cooke 1987, Finney and Cooke 1978, Rockwell et al. 1983).

Egg-volume estimation.-We collected a sample of 51 and 90 unhatched eggs in 1988 and 1989, respectively. The contents of these addled, infertile, or abandoned eggs were removed, and the shells were dried. External volume was measured by sealing the holes in the shell with Parafilm, submerging the egg, and measuring the displacement of water to the nearest 0.5 cm^3. Submersion was

accomplished with a fine wire that had negligible displacement (<0.25 cm^3). Internal volume was estimated by taring the sealed shell mass, filling the egg with distilled water, and reweighing. A measured quantity of distilled water was weighed and water density was assumed to be constant (1 g/cm^3). Parameters in the relationship between external measures of length and width and the measured volumes were estimated using Hoyt's (1979) equation. To estimate egg-shell thickness, eggs were cut in half longitudinally and shell thickness was measured to the nearest 0.01 mm with dial calipers. Shells were measured at both ends and at the midpoint of the long axis.

Statistical analysis.-Variation in mean egg volume among years and among clutches of three, four, and five eggs was examined using a two-way analysis of variance (ANOVA). The relationship between egg volume and position in the laying sequence was examined using nested ANOVA, with clutches as the nested factor. The relationship between egg size and nest initiation date was compared among years using a one-way analysis of covariance (ANCOVA), with year as a factor and nest initiation date as a covariate. We estimated repeatability of egg size, clutch size, and clutch volume using a one-way ANOVA to partition the variance into within- and among-individual components and then applied the equations of Lessells and Boag (1987). Standard errors of the repeatability estimates were calculated following Becker (1984).

Clutch size and egg size were compared for two-year-old and older females using a multivariate Hotellings T^2. Dates of nest initiation of two-year-old females were compared with those of older females with a *t*-test. A two-way ANCOVA on egg size grouped by year and clutch size, excluding females younger than age 3, with initiation date as a covariate, was used to assess the

effects of age on the relationship of egg size and initiation date. All analyses were done using BMDP statistical software (Dixon 1985).

Results

Estimation of egg volume.-The relationship between external volume and linear egg measurements was described by the equation:

$$V_{ex} = 8.22 + (0.4636\, LB^2)/1{,}000,$$

where V_{ex} is external volume in cm^3, L is length in millimeters, and B is breadth in millimeters ($r^2 = 0.92$, $P = 0.0001$). Analysis of covariance indicated no annual difference in this relationship for eggs collected in 1988 and 1989 ($F_{1,132} = 0.17$, $P = 0.68$). Analysis of covariance on the same form of equation fit to internal volumes, revealed significant differences in the slopes of the regression coefficients for eggs collected in 1988 versus 1989 ($F_{1,132} = 6.44$, $P = 0.012$). Mean shell thickness (grand mean of three points from each egg) did not differ between years, ($t = 1.27$, $df = 132$, $P = 0.20$). However, when the three individual point measurements were considered separately, eggs from 1988 were significantly thicker at the large end of the long axis than eggs from 1989 ($t = 2.27$, $df = 132$, $P = 0.008$). No significant between year differences occurred at the other two points of measurement ($P > 0.15$).

External volumes of eggs measured in the field were estimated from the fitted relationship between external volume and linear measurements. A total of 3478 eggs was measured over three seasons. Mean egg volume was 84.0 SE of 5.74 cm^3 (range 57.5-103.1 cm^3). We compared the estimated volumes of the collected eggs to the entire sample of measured eggs to determine if collected eggs were a representative sample of eggs from the entire population. Eggs

collected for determination of volume in 1988 did not differ from the sample of eggs measured in that year ($t = 1.42$, $df = 1203$, $P = 0.15$); however, eggs collected in 1989 were significantly smaller than those measured in the field ($t = 3.50$, $df = 2120$, $P = 0.0005$).

Variation in egg size.-Egg volume varied significantly with clutch size ($F_{2,2317} = 5.77$, $P = 0.0032$), and year ($F_{2,2317} = 7.30$, $P = 0.0007$). Smaller eggs were laid in 1988 and 1989 than in 1987, and larger eggs were laid in larger clutches (Fig. 1). As indicated in figure 2, egg volume declined significantly with laying sequence for clutches of three, four, and five eggs, ($F_{1,109} = 28.23$, $P = 0.0001$; $F_{1,224} = 9.59$, $P = 0.002$; $F_{1,219} = 29.39$, $P = 0.0001$, respectively). Egg size declined significantly with date of nest initiation after controlling for clutch size and year effects ($F_{1,430} = 9.78$, $P = 0.0019$).

There was overlap in total estimated clutch volume among clutches of different sizes (Fig. 3). Clutch size explained 92% of the variation in total clutch volume ($r^2 = 0.918$, $P = 0.0001$). Absolutely and relatively more females laid clutches of fewer large eggs than vice versa in both zones of overlap. The range of average egg sizes were essentially the same for clutches of three, four, and five eggs (70.0-94.3 cm^3, 69.0-94.8 cm^3, 72.6-99.6 cm^3, respectively).

Repeatability and age related variation.-Repeatabilities of egg size, clutch size and clutch volume of females older than three-years were 0.78 0.077 (SE) ($F_{24,27} = 8.444$, $P = 0.0001$), 0.14 0.10 ($F_{74,92} = 1.359$, $P = 0.08$), and 0.14 0.23 ($F_{17,19} = 1.347$, $P = 0.26$), respectively. Two-year-old females laid significantly smaller clutches of smaller eggs than did older females ($T^2_{2,289} = 15.97$, $P = 0.0004$). Additionally, two-year-old females initiated nesting significantly later than did older females ($t = 2.93$, $df = 92$, $P = 0.0042$).

However, after restricting the analysis to females older than two-years, egg size still declined with nest initiation date ($F_{1,61} = 6.41$, $P = 0.014$).

Discussion

Predictive equations.-In 1989, the sample of unhatched eggs for which we determined volumes was significantly smaller than the entire sample of measured eggs. This suggests that smaller eggs had lower viability, or that females producing small eggs were less likely to hatch their clutches in that year. Similar observations of lower hatching success among small eggs have been reported in other birds (Martin and Arnold 1991). The range in volume of eggs for which we measured volume directly included all but 7 cm^3 of the range of predicted volumes of eggs we measured in nests. Thus, estimated egg volumes (based on linear measurements) were extrapolated only 7.3% above, and 10.5% below the size range of eggs from which we obtained our predictive equation. Further, the lack of annual variation in the equations used to estimate external volume from linear measures suggests that, while egg volume may have varied, egg shape did not. Therefore, we believe that the calculated external egg volumes in our analysis provide accurate estimates of true egg volumes.

Variation in shell thickness.-Annual variation in the relationship between egg measurements and internal shell volume must have been caused by variation in patterns of egg-shell thickness, because the relationship between external volume and egg measurements did not exhibit such annual variation. Shells differed in thickness between years at only one measured point, which changed the internal volume relative to external measurements. The cause of shell thinning in 1989 at one location on the shell is unknown. Eggs were larger with resulting

larger shell surfaces in 1988 than in 1989, which potentially magnified the between year difference in the amount of calcium deposited in each egg. Annual variation in calcium available to females might have caused the variation in shell thickness among years.

Within-clutch variation in egg volume.-The same general relationship between egg size and position in the laying sequence that we observed in Black Brant has been reported for Canada Geese (Branta canadensis maxima, Cooper 1978; B. c. moffitti, Leblanc 1987) and American Coots (Fulica americana, Arnold 1991). Also, Cargill (1979) reported that the last egg was the smallest in clutches of Lesser Snow Geese (Anser caerulescens caerulescens). The increase in size of the second egg relative to the first in clutches larger than three eggs may be related to physiological or morphological constraints on the size of the first egg. Parsons (1976) showed that egg size increased between the first and second egg in initial clutches of Herring Gulls (Larus argentatus), but not in clutches from renesting attempts, suggesting that the first laid egg of the season is small, but not necessarily the first laid egg in all clutches. However, the lack of an increase in egg size in three-egg clutches does not support this hypothesis, unless some fraction of three egg clutches represent continuation clutches for which the first egg was laid elsewhere. This hypothesis can perhaps best be examined in captive waterfowl that can be induced to renest.

Consistent with Arnold (1991), we do not believe that the decline in egg size with laying sequence is a response to limited nutrient reserves (Alisauskas and Ankney 1985). Leblanc (1987) observed a similar pattern of declining intraclutch egg size among captive Canada Geese fed ad libitum. Further, variation among wild females in the total reserves available for laying should allow some females to lay a clutch with little or no reduction in egg size, while others

could show a substantial decline in egg size. If declining nutrient reserves during egg laying explain the decline in egg size, then variation in the size of reserves available to individual females should increase the variation in egg size with increasing egg number, especially for the last-laid egg (Slagsvold et al. 1984). This is because some females should have more reserves remaining than required for one egg but insufficient reserves for two additional eggs. These females should lay large last eggs under the hypothesis that remaining reserves influence egg size. In contrast, females with fewer reserves than required for an average egg should lay a smaller egg. The net effect of these two influences would be increased variation in the size of the last egg. We did not observe increased variation in egg size with egg number (Fig. 2). Therefore, the nutrient limitation hypothesis is not consistent with the observed pattern of intraclutch variation in egg size.

Parsons (1972) hypothesized that the intraclutch decline in egg size in gulls may be an adaptation to synchronize hatch. We propose that this hypothesis may also apply to the intraclutch egg size variation in Black Brant. First-laid eggs in Black Brant receive substantial incubation during the laying of subsequent eggs (P. L. Flint and M. S. Lindberg unpubl. data). Smaller eggs require less incubation (Worth 1940, Parsons 1972, Martin and Arnold 1991); thus, a reduction in egg size for later eggs in a clutch could help synchronize hatching within clutches.

Temporal and clutch size related variation in egg size.-Annual variation in egg size has been observed in Lesser Snow Geese (Newell 1988), Canada Geese (Cooper 1978), and Black Brant (Rohwer and Eisenhauer 1989). Cooper (1978) suggested that annual variation in the age structure of the population might explain variation in mean egg volumes among years. This could also explain the pattern we observed in Black Brant. Eggs hatched in only 2% and 7% of the

nests on the Tutakoke River colony in 1984 and 1985, respectively (J. S. Sedinger unpubl. data). Nesting success increased substantially following removal of Arctic foxes (Alopex lagopus) beginning in 1986 (Anthony et al. 1991). Female Black Brant tend to return to their natal colony to breed (J. S. Sedinger and P. L. Flint unpubl. data); thus, the proportion of two- and three-year-old females in the breeding population should have increased during each year of this study. Because two-year-old females laid smaller eggs than older females, the reduction in egg size among years was associated with, and could have resulted from, a higher proportion of two- and three-year-old females in the breeding population in 1989. Rohwer and Eisenhauer (1989), however, observed annual variation in egg mass in a population of Black Brant that was relatively stable in size and, thus, could have had a stable age distribution.

The positive relationship between mean egg volume and clutch size found by us and by Rohwer and Eisenhauer (1989) could have resulted from variation in female age. Two-year-old females laid smaller clutches of smaller eggs compared to older females. The positive correlation between egg volume and clutch size may have resulted from the positive relationships between age and clutch size, and age and egg size (i.e. small clutches were disproportionately produced by two-year-old females who also laid smaller eggs).

The cause of the seasonal decline in egg size after accounting for age is unknown. Hill (1984) observed a comparable seasonal decline in egg size of Tufted Ducks (Aythya fuligula), which he attributed to younger females laying later. Age did not completely explain the seasonal decline in egg size in Black Brant, however, because egg size also declined with initiation date after two-year-olds were eliminated from the analysis. Thus, the observed decline was not strictly related to two-year-old females nesting later. However, age-specific

variation in egg size of Black Brant has not been documented, and egg size may continue to increase beyond age two. Additionally, previous breeding experience may influence egg size, and we could not control for experience. Thus, the effect of age and/or breeding experience on the seasonal decline in egg size deserves further consideration. An alternative hypothesis, that the reduction in egg size with laying date was caused by reduced nutrient reserves among late or delayed-nesting females, seems unlikely because the high repeatability of egg size (see below) suggests that females do not alter egg size in relation to their nutritional status.

Clutch size did not completely explain the variation in total clutch volume (Fig. 3). Clutches of different sizes overlapped in the volume of reserves invested. The relative size of the zones of overlap we observed in Black Brant are considerably smaller than those reported for Lesser Snow Geese (Ankney and Bisset 1976), despite the slightly smaller sample sizes for Lesser Snow Geese. The size of the zones of overlap is ultimately determined by variation in egg size in the population. The coefficient of variation in egg size we observed in Black Brant (0.063) is smaller than that reported for egg mass in Lesser Snow Geese (0.075; Newell 1988). Therefore, the smaller zones of overlap that we observed may be due to greater normalizing selection on egg size in Black Brant.

Repeatabilities.-The high repeatability of egg volume in Black Brant is consistent with that reported in other species of waterfowl (Batt and Prince 1979, Duncan 1987, Lessells et al. 1989). However, the high repeatability of a trait that may be related to fitness (P. L. Flint and J. S. Sedinger unpubl. data; Cole 1979, Newell 1988) is difficult to reconcile with theory (Mousseau and Roff 1987). The lower repeatability of clutch size is also consistent with the literature (Lessells et al. 1989) and the low repeatability of clutch volume is probably a result of the low

repeatability of clutch size. The repeatability for clutch volume could only exceed that for clutch size if females were flexible in their phenotypic egg size.

If stored nutrients limit clutch size, then the low repeatability of clutch size and clutch volume suggests that individuals are highly variable in their condition on arrival. Thus, while reserves are correlated with body size (Ankney and MacInnes 1978), condition of individual females at the start of laying must vary sufficiently among years to alter clutch size.

Our inability to detect egg dumping in clutches used in the repeatability analysis must have increased the within-female variation in our repeatability estimates of both egg size and clutch size. Thus, we may have underestimated the true repeatability of clutch size and egg size. Undetected partial predation had little effect on the estimated repeatabilities for egg size, however, it would have caused us to underestimate repeatability of clutch size.

Relationship between clutch size and egg size.-Consistent with our results, Rohwer (1988) and Rohwer and Eisenhauer (1989) failed to find negative phenotypic relationships between clutch size and egg size within several populations of waterfowl. Further, Lessells et al. (1989) did not find negative phenotypic or genotypic covariances between clutch size and egg size in Lesser Snow Geese. They argued that their results failed to support the hypothesis of a trade off between clutch size and egg size and, thus, the nutrient limitation hypothesis for control of clutch size in waterfowl.

While we also failed to detect a trade off between clutch size and egg size, we find several points interesting. First, females laying different clutch sizes produce approximately the same range of egg sizes (Fig. 3). We expected that large egg size phenotypes would be less likely to lay large clutches, unless larger females lay larger eggs and have larger nutrient reserves. We have not, however,

detected a relationship between body size and egg size in Black Brant (J. S. Sedinger unpubl. data).

Second, where clutch volumes overlap for clutches of different size (e.g. four and five eggs) females laying different clutch sizes are making the same investment in their clutches. In these zones of overlap, where investment in the clutch is held constant, there is a trade off between clutch size and egg size. Thus, trade offs have not been found among individuals with different investments in their clutch (i.e. differences in mean egg size across clutch sizes) (Rohwer 1988, Rohwer and Eisenhauer 1989), yet they do occur among individuals with the same investment in their clutch (i.e. zones of clutch volume overlap). However, only the extreme egg size phenotypes, a small proportion of the total population, are engaged in this second form of trade off.

Finally, the use of stored reserves, the high repeatability of egg size, and the low repeatability of clutch size are all conditions which should allow the detection of a trade off between clutch size and egg size among females with different investments in their clutch (Rohwer and Eisenhauer 1989). Thus, our inability to detect trade offs between egg size and clutch size among females with different investments in their clutches, argues against the nutrient limitation hypothesis as the sole mechanism regulating clutch size in the Black Brant.

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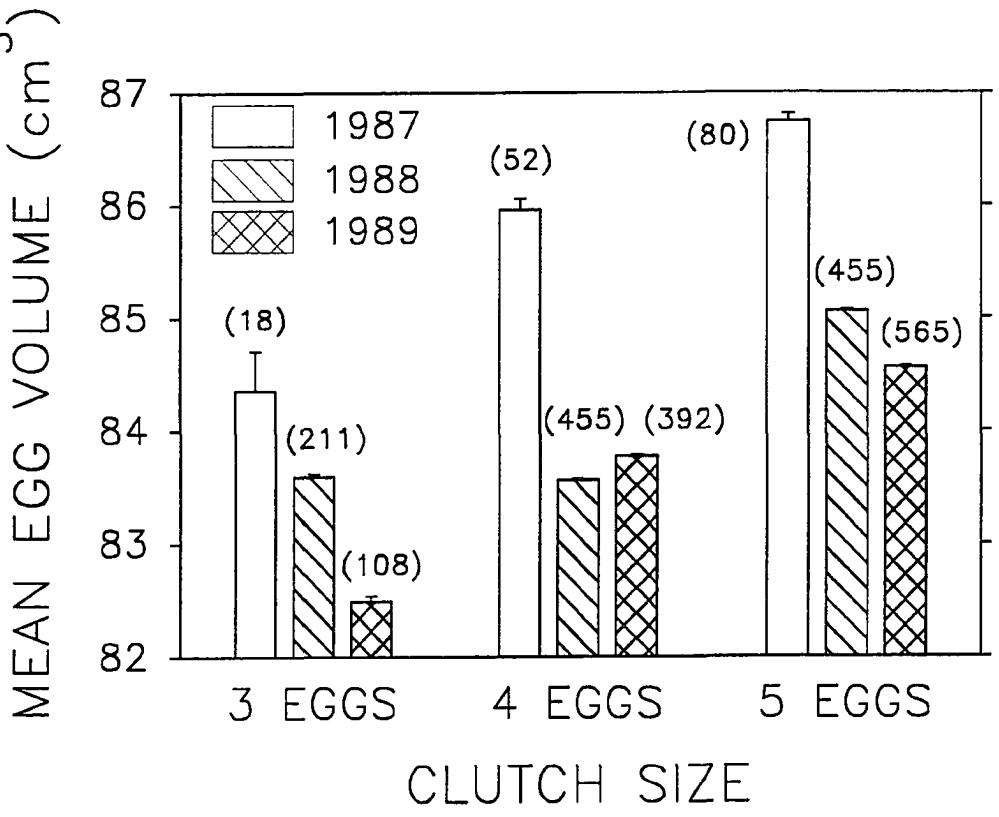
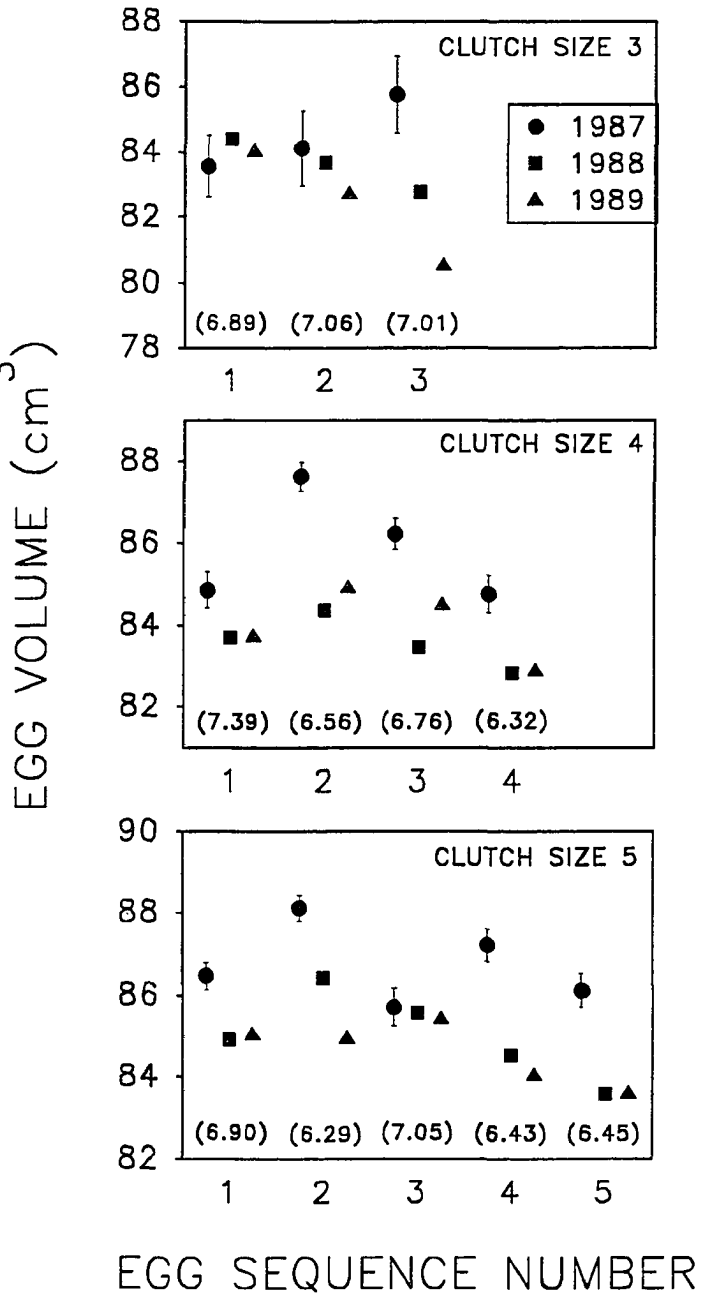
Figure Legends:

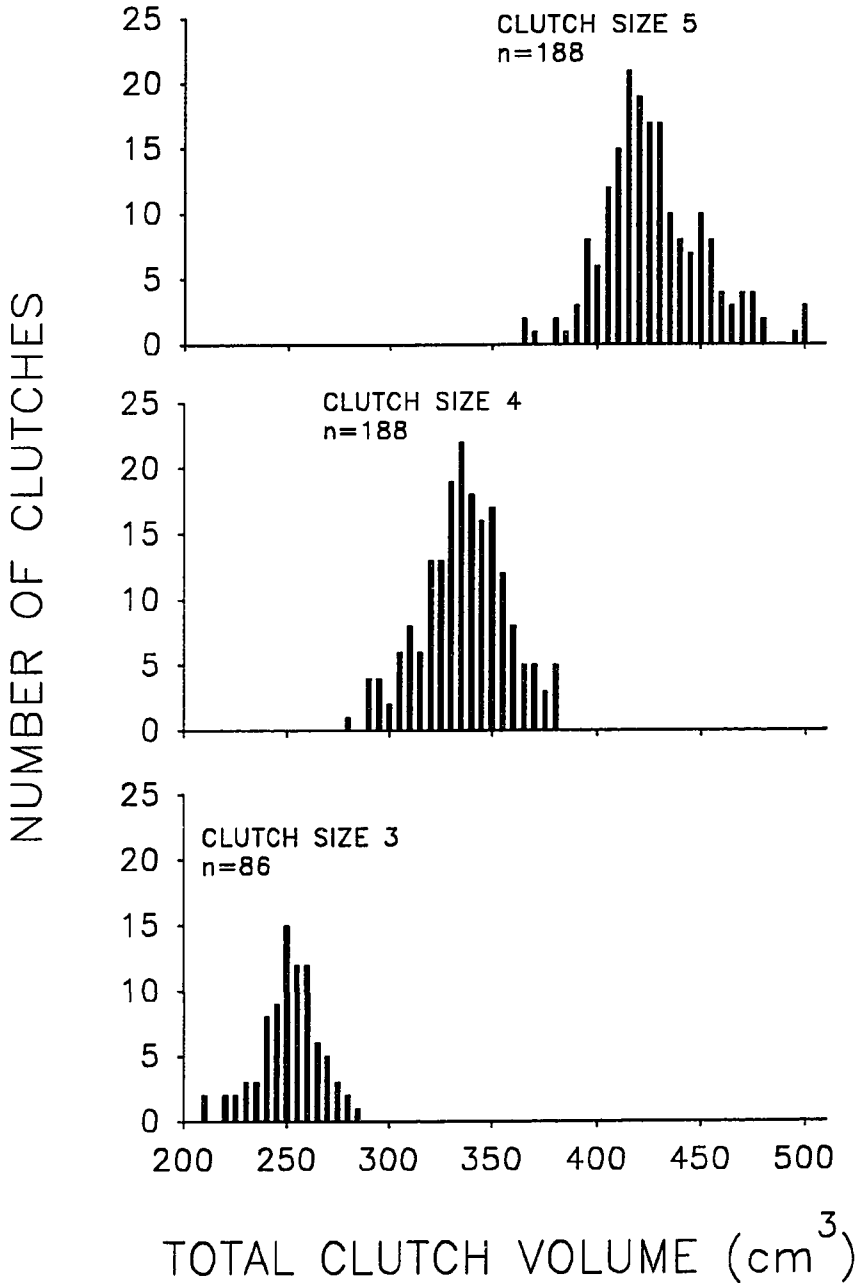
Fig. 1. Mean (bars indicate SE) egg volume for clutch sizes of three, four, and five eggs in 1987, 1988, and 1989. Egg volume varied significantly among clutch sizes and years (P = 0.0032 and 0.0007, respectively). Sample sizes in parentheses. Error bars less than 0.01 were not plotted.

Fig. 2. Mean (SE) egg volume versus laying sequence for clutches of three, four, and five eggs. There was a significant difference in egg volume with laying sequence within all clutch sizes (P = 0.0001, 0.002, 0.0001, respectively). Error bars less than 0.1 were not plotted. Average coefficient of variation for each egg number presented in parenthesis. Minimum sample size for each egg number in clutches of three, four, and five eggs in 1987 were 6, 10, and 12, respectively. Similarly, minimum sample sizes for 1988 and 1989 were 67, 110, 85, and 32, 87, 103, respectively.

Fig. 3. Overlap in total clutch volume for clutches of three, four, and five eggs. Zones of overlap define ranges of reproductive investment where females with different egg size phenotypes engage in trade offs involving clutch size and egg size.







Survival of prefledging black brant: effects of initial brood size, egg size, and hatch date

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Running Head: black brant gosling survival

Summary

1. We web-tagged black brant (Branta bernicla nigricans) goslings at hatch, recorded their egg size, position in the egg-laying sequence, initial brood size, hatch date, and nesting density, and examined the effect of these characteristics on their probability of recapture.

2. Goslings from larger eggs, and larger initial broods, and with earlier hatch dates were more likely to be recaptured.

3. The relationship between laying position within the clutch and gosling recapture varied with clutch size; laying position was significantly related to the probability of recapture only in 4-egg clutches.

4. There was a tendency for young females to be less successful in rearing their broods; however, this may be related to their egg size, initial brood size, and hatch date, rather than age per se.

Key-words: black brant, brood rearing success, age, egg size, hatch date, brood size.

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Introduction

Survival of young to fledging is an important, yet highly variable, component of reproductive success in waterfowl (Anseriformes). Our earlier study assessing survival of juvenile black brant (Branta bernicia nigricans) estimated that only 64% of the hatchlings survive to fledging, and 20% of the successfully nesting adult population fledge no young in a given year (Flint & Sedinger, unpublished). Parental age, breeding experience, and body condition can influence annual reproductive success (Gauthier 1989; Forslund & Larsson 1992). Survival in young waterfowl also is influenced by extrinsic factors such as predation and environmental conditions (Mendenhall & Milne 1985; Owen & Black 1990), and intrinsic factors such as egg size, hatch date, brood size, and position in the hatching sequence (LeBlanc 1987; Gauthier 1989; Forslund & Larsson 1992).

Previous research has suggested that survival in young waterfowl may be related to their egg size or position in the laying sequence (Kear 1965; Cole 1979; Ankney 1980; Rhymer 1988; Thomas & Brown 1988); however, these relationships have rarely been demonstrated in wild populations. Cole (1979) reported that lesser snow goose (Anser caerulescens caerulescens) goslings from small eggs were less likely to be recaptured than those from large eggs in 1 of 2 years sampled. Internal energy reserves of hatching waterfowl and their fasting endurance have been shown to be positively correlated with egg size (Kear 1965; Ankney 1980; Rhymer 1988; Thomas & Brown 1988). Additionally, egg size has a weak positive effect on the growth rate of black brant goslings (Sedinger & Flint 1991). In waterfowl clutches, eggs typically hatch in the order in which they are laid (Prince, Siegel & Cornwell 1969; Cargill & Cooke 1981) and hatching success declines with increasing developmental asynchrony (Kennamer, Harvey & Hepp 1990). Moreover, hatching asynchrony creates a situation in

which late hatching young are more likely to be abandoned in the nest or lost during initial brood movements (LeBlanc 1987). Consequently, position in the egg laying sequence may influence gosling survival.

Previous research has indicated that hatch date may effect juvenile survival in waterfowl (Dow & Fredga 1984, Findlay & Cooke 1982a). Hatch date has been shown to be negatively associated with juvenile survival to fledging in goldeneyes (Bucephala clangula, Dow & Fredga 1984); however, Gauthier (1989) reported no relationship between hatch date and juvenile survival in buffleheads (B. albeola). Findlay & Cooke (1982a) showed that lesser snow geese hatching near the mean for the colony survived to fledging at the highest rate. Hatch date is negatively associated with gosling growth rate in black brant and lesser snow geese (Sedinger & Flint 1991; Cooch et al. 1991), indicating declining foraging conditions during brood rearing. This nutritional stress might reduce survival as well as growth of late hatching goslings.

The effect of brood size on survival of young is poorly understood for waterfowl. Several studies have shown no relationship between brood size and survival (Heusmann 1972; Clawson, Hartman & Fredrickson 1979; Rohwer 1985; Lessells 1986). In contrast, others reported a reduction in survival for goslings in large broods (MacInnes et al. 1974; Andersson & Eriksson 1982; LeBlanc 1987; Rockwell, Findlay & Cooke 1987; Winterstein 1992). Large broods may be easier for predators to detect and successfully attack (Safriel 1975).

Black brant nest in colonies with highly variable local densities (Welsh 1988). Advantages of colonial nesting in black brant may extend to the early brood rearing period, because broods moving through high density nesting areas may inadvertently receive protection from avian predators by neighboring broods. Broods from high density areas could also benefit from predator swamping.

Further, broods from high density areas may be more likely to form brood flocks, thereby further reducing the risk of predation (Findlay & Cooke 1982a).

Female age and breeding experience can influence reproductive success. Younger and less experienced females typically have lower reproductive output (Finney & Cooke 1978; Gauthier 1989; Afton 1984; Forslund & Larsson 1992; Dow & Fredga 1984). Brood rearing success is an important component of overall reproductive success. Younger females may be less successful in rearing their broods due to their inexperience, or their lower investment in the reproductive attempt (Forslund & Larsson 1992) (i.e. 2-year-old female brant lay smaller clutches of smaller eggs than older females, Flint & Sedinger 1992).

An individual's fitness is measured as the number of offspring recruited into the breeding population (Falconer 1989). Thus, juvenile survival between hatching and fledging is a measure of only one component of fitness. Measurement of incomplete selection gradients for life-history characteristics, however, can improve our understanding of potential bottlenecks and shifts in selection gradients across time periods. The effect of the selection gradients observed between hatch and fledging may be magnified by continuing selection, maintained by a lack of selection, or canceled by opposing selection pressure after fledging.

Our goal in this study was to examine female reproductive tactics and characteristics that influenced survival of black brant goslings. We examined the effects of initial brood size, egg size, hatch date, egg position in the laying sequence, and nesting density on recapture rates at fledging of broods with goslings webtagged at hatch. Additionally, we examine the effect of female age on brood rearing success.

Methods

This study was conducted during the summers of 1987-1990 on the black brant colony located at the mouth of the Tutakoke River (61°15' N, 165°37' W) on the outer coastal fringe of the Yukon Delta National Wildlife Refuge in western Alaska. Nesting occurs in wet sedge meadows dominated by Carex ramenskii, several hundred meters inland from the mudflats of the Bering Sea coast. After hatch, broods move to the vegetation-mudflat interface and feed on short sedges and grasses, such as C. subspathacea and Puccinellia phryganodes. A detailed description of the vegetation is provided by Kincheloe & Stehn (1991). Broods may move along the coast or major tidal sloughs up to 25 km from the colony.

NESTING

We located nests by searching randomly located circular plots (50 m radius) every fourth day from nest initiation through the completion of egg laying. Nests were marked, mapped on aerial photos, and assigned a unique number. Laying sequence was determined by the degree of shell staining (Flint & Sedinger 1992) and each egg was labeled with permanent marker. If eggs could not be differentiated based on staining, we did not assign eggs a position in the laying sequence. Maximum length and breadth of all eggs were measured to the nearest 0.1 mm using dial calipers.

We searched the entire colony during incubation to associate individually marked females with their nests. These females were marked in previous years with uniquely encoded 2.5 cm wide plastic tarsus bands. Females were flushed from nests and their tarsus band codes, if present, were recorded. The age of females originally banded as goslings could then be determined. Black brant can be aged by feather characteristics through 1 year of age (Harris & Shepherd

1965). Thus, females with adult plumage when originally banded are known to be at least 2 years old. This criterion was used to establish minimum ages for all females marked after their first year. We used age classifications of 1, 2, 3, and >3 years, because goslings banded in 1986 provided our oldest sample of known-age females (4 years-old), however, this was a small sample (n=9). Eggs in nests of marked females were measured as previously described.

Nests on plots, nests of marked females, and nests encountered incidentally throughout the colony were visited during hatching. Individually coded webtags were placed on hatched goslings or those in pipped eggs (Alliston 1975). Nests known to contain hatching eggs were then avoided for 48 h to reduce the likelihood of premature departure of the brood. Linear dimensions of pipped eggs from nests located during hatching were measured as previously described. Egg dimensions were converted to egg volumes based on the relationship between length*width^2 and egg volume (Hoyt 1979) from a sample of collected eggs (Flint & Sedinger 1992).

We calculated relative hatch dates for each year by subtracting hatch dates from the date of peak of hatch for that year. Therefore, we controlled for differences in timing of spring break-up and nesting among years. After hatch was complete and broods had moved off of the colony, the distance from a sample of nests to the two nearest neighboring nests was measured to the nearest 0.1 m. We used the mean of these two measures as an index of local nesting density for each nest.

Broods were herded into corral traps between 26 and 34 days after the peak of hatch. All goslings were inspected for the presence of webtags, which were recorded. A sample of juveniles and adults (n=2,000-2,800) was banded to increase sample sizes in future years.

STATISTICAL METHODS

Because of the potential lack of independence of survival among brood mates (Winterstein 1992), we used broods as our sampling units. Thus, goslings from a given brood were pooled, and the proportion of each brood recaptured was calculated. Egg size varies relatively little within clutches compared to variation among clutches (Flint and Sedinger 1992); therefore, the mean egg size for the brood was used.

We were unable to measure all independent variables (e.g. egg size, initial brood size, hatch date, and nesting density) for all nests in which goslings were webtagged. Hatch date was known for all clutches for which we webtagged goslings. Initial brood size was estimated only for nests in which all goslings could be webtagged (i.e. those located during the latter stages of hatching when the last egg was at least pipped). Egg size was only known for clutches containing pipped eggs, and nesting density was determined for a sample of nests on random plots and nests of marked females. Correlations among the measured variables were small ($r < 0.18$ for all pairwise relationships). To maximize sample size and therefore power, and because the variables were not highly correlated, we used only univariate tests of the variables.

We performed 3 different analyses to assess the effects of the independent variables on survival. First, we used t-tests to test the null hypothesized that the means of the independent variables (e.g. hatch date) for recaptured and unrecaptured broods were the same. To determine if the pattern in survival was the same across years, we used a 2-way analysis of variance to assess the interaction between success and years. Because we recaptured only a fraction of the population at banding, a substantial number of surviving webtagged goslings were not recaptured (e.g. we recaptured 28% of the marked broods compared to

an average brood success of 83%; Flint & Sedinger, unpublished). We assumed that we recaptured a random sample of the population of broods surviving to fledging. Under directional selection, as opposed to stabilizing or disruptive selection, these analyses are conservative with respect to the relationship between the variable in question and gosling survival.

In our second analysis, we tested the null hypothesis that we recaptured at fledging a random sample of the broods marked at hatch with respect to each independent variable. We used a heterogeneity χ^2 goodness of fit approach to compare the broods with at least one recaptured gosling to the entire population of tagged broods across years (Zar 1984). If the heterogeneity χ^2 was not significant ($P > 0.05$), years were pooled. For these analyses, we grouped continuous variables, egg size, hatch date, nesting density, into three categories with approximately equal sample sizes of broods marked. The expected cell frequencies were calculated by the cell percent from the marked population times the number recaptured.

In our third analysis we tested the null hypothesis that the number of goslings recaptured for each brood was unrelated to the independent variables. We examined variation in survival within broods for which at least one gosling was recaptured by comparing the number of goslings recaptured from a given brood with the expected number recaptured if the variable of interest had no effect on the probability of recapture (see Rockwell, Findlay & Cooke 1987). The expected number recaptured was determined by multiplying the mean proportion recaptured by the number of goslings marked in each brood. Deviation from the expected number recaptured was calculated as the actual number recaptured minus that expected for each brood. These deviations were then regressed against the variable under consideration for continuous variables (e.g. egg size,

hatch date, nesting density). Deviations for discrete (e.g. initial brood size, female age) variables were compared among categories with ANOVA.

The effect of egg sequence number on the probability of recapture was analyzed using a one-way analysis of covariance (ANCOVA) to compare the mean proportion recaptured among egg sequence numbers with egg size as a covariate. This analysis used individual goslings as the sampling unit and each clutch size was considered separately. This analysis was also restricted to the subset of broods for which at least one gosling was recaptured, thus comparing captured individuals with their un-recaptured brood mates.

Results

EGG VOLUME

The mean egg volume of broods that had at least one gosling recaptured was significantly ($t_{813}=2.01$, $P=0.0444$) greater than for broods with no goslings recaptured (Table 1). We detected no interaction between egg volume and year ($F_{3,807}=1.90$, $P=0.1279$). The number of broods recaptured from each egg size category did not differ from a random sample of the marked population ($\chi^2_{2df}=2.65$, $P=0.5$), although the pattern was in the expected direction if large eggs improved early survival (Fig. 1). There was no relationship between the deviations from the expected number recaptured and the mean egg volumes of broods ($F_{1,221}=0.152$, $P=0.70$).

HATCH DATE

The mean relative hatch date of broods that had at least one gosling recaptured was significantly ($t_{1149}=2.22$, $P=0.0267$) earlier than for broods with no goslings

recaptured (Table 1). We detected no interaction between the effect of relative hatch date and year ($F_{3,1143}=1.65$, $P=0.1760$). The number of broods recaptured from each hatch date category (early, middle, and late) did not differ significantly from a random sample of the marked population ($\chi^2_{2df}=4.378$, $P=0.09$), although the observed number of broods recaptured with early hatch dates exceeded the number expected (Fig. 1). There was no relationship between the deviations from the expected number of goslings recaptured and hatch date ($F_{1,309}=0.627$, $P=0.429$).

NESTING DENSITY

Nesting density of broods with at least one recaptured gosling was not significantly ($t_{725}=0.65$, $P=0.5295$) different from broods with no goslings recaptured (Table 1). We detected no interaction among years ($F_{3,719}=1.03$, $P=0.3789$). The number of broods recaptured from each nest density category did not differ from a random sample of the marked population ($\chi^2_{2df}=0.7354$, $P=0.8$) (Fig. 1). The analysis comparing deviations from the expected number of goslings recaptured also showed no significant trend across different nesting densities ($F_{1,192}=0.159$, $P=0.6902$).

INITIAL BROOD SIZE

Initial brood size (number of goslings leaving the nest) of broods with at least one recaptured gosling was significantly ($t_{1139}=2.21$, $P=0.0274$) larger than that of broods with no goslings recaptured (Table 1). We detected no interaction with year ($F_{3,669}=0.96$, $P=0.4134$). The initial brood size distribution of recaptured broods was significantly different from a random sample of the marked population ($\chi^2_{2df}=6.537$, $P=0.04$). The observed number of broods with large initial brood

sizes exceeded the number expected (Fig. 1). There was a significant negative trend in survival within broods with increasing initial brood size (Fig. 2) ($F_{4,316}$=6.1556, P=0.0001). The proportion of goslings recaptured was 0.1693, 0.1390, 0.1392, for initial broods of 3, 4, and 5 goslings, respectively.

FEMALE AGE

Broods with at least one gosling recaptured tended to be associated with older females than broods that had no goslings recaptured (t_{341}=1.84, P=0.1007). We had insufficient samples of known age females to test for an interaction between age and year effects. The number of broods recaptured from each age class did not differ from a random sample of the marked population (χ^2_{3df}=3.054, P=0.3000) (Fig. 1). No significant relationship existed between deviations from the expected number of goslings recaptured and age of females attending broods ($F_{2,111}$=0.3313, P=0.7187).

EGG SEQUENCE

The relationship between the probability of gosling recapture and egg sequence number and egg size varied among clutch sizes. In 3-egg clutches, recaptured goslings came from larger eggs (t_{74}=2.050, P=0.044) but recapture was unrelated to egg sequence number ($F_{2,73}$=1.381, P=0.258). In 4-egg clutches recaptured goslings were more likely to come from the earlier laid eggs ($F_{3,370}$=3.085, P=0.029) but there was no relationship to egg size (t_{172}=0.375, P=0.708). In 5-egg clutches, neither egg size nor egg number varied significantly with respect to recapture of goslings (t_{259}=0.40, P=0.687; $F_{4,256}$=0.534, P=0.711, respectively).

Discussion

INTERPRETATION OF ANALYSES

We used three different analyses to examine factors associated with survival of goslings between hatching and fledging. Two analyses, comparison of mean attributes of broods with at least one versus no recaptured goslings, and goodness-of-fit comparisons of marked and recaptured broods, consider broods as either completely successful or unsuccessful only. These analyses ignore within brood variation in the number of goslings recaptured. Thus, these methods are only sensitive to relationships between total brood loss and the variable of interest. The third analysis compares the expected number of goslings recaptured with the actual number recaptured for broods with at least one gosling recaptured. This method tests the relationship between partial brood loss and the variable of interest. These two analyses, total versus partial brood loss, measure different, although not independent, components of overall survival.

EGG SIZE

Black brant goslings from larger eggs survived at a higher rate than those from smaller eggs; however, overall evidence for this pattern was weak. Cole (1979) reported that lesser snow goose goslings from small eggs were less likely to be recaptured in only one of two years sampled. In our study, however, the pattern of survival relative to egg size was consistent among years. Our findings are consistent with others showing that egg size is positively correlated with internal food reserves and fasting endurance in goslings (Ankney 1980; Kear 1965; Rhymer 1988; Thomas & Brown 1988). Additionally, young mallards (Anas platyrhynchos) from larger eggs can maintain homeothermy at colder environmental temperatures than can ducklings from smaller eggs (Rhymer

1988). The relationship between egg size and cold tolerance, food reserves, and persistence should affect the ratio of feeding to brooding time for young goslings and thus early gosling survival and growth.

HATCH DATE

Goslings hatching during early and median periods tended to survive better than those hatching later, although evidence for this pattern was weak. A similar pattern of juvenile survival relative to hatch date exists in goldeneyes (Dow & Fredga 1984). Findlay & Cooke (1982a) hypothesized that goslings hatching near the mean for the colony would survive better due to predator swamping. The overall pattern in survival that we observed (Fig. 1) supports this hypothesis as the highest recapture rate was for broods hatching near the colony mean. Nonetheless, we recaptured more early hatching broods than expected; under this hypothesis such broods gain the least from predator swamping. The greatest loss that we observed was of late hatching young which, on a colony level, should benefit the most from predator swamping. Although, higher survival of broods hatching near the median is consistent with the hypothesis of Findlay & Cooke (1982a), we do not believe predator swamping is the principal factor explaining the observed pattern.

Alternatively, forage quality and availability begin declining during the hatching period and late hatching young are at a nutritional disadvantage (Sedinger & Raveling 1986). This decline in forage quality and availability is a likely cause of the slower growth rate of late hatching goslings (Cooch et al. 1991; Larsson & Forslund 1991; Sedinger & Flint 1991). We hypothesize that the higher mortality of late hatching young may also be related to declining foraging conditions. This nutritional disadvantage could influence survival directly but most

likely exacerbates the effects of predation and weather conditions on gosling survival.

NESTING DENSITY

The lack of any relationship between local nesting density and gosling survival suggests that factors favoring colonial nesting occur before hatching or are unrelated to gosling survival. We were unable, however, to assess the actual nesting density on the date when broods moved off of their territories, or synchronization in hatch date among neighbors, both of which could have affected the magnitude of protection received during initial brood movements. Thus, our index of nesting density may have been inadequate, especially during the immediate post hatching period when nesting density was most likely to be important.

INITIAL BROOD SIZE

Females with larger initial broods were more likely to fledge at least one young. Nevertheless, the per gosling probability of surviving from hatching to fledging was highest for goslings from broods of 3, and lowest for goslings from broods of 4 and 5. This same negative trend in gosling survival with increasing brood size and increasing brood success with increasing brood size has been observed in lesser snow geese (Rockwell, Findlay & Cooke 1987). The average number of goslings recaptured from broods of each size provides an index of relative production from different clutch sizes. This index of production in terms of the number of goslings fledged, given the proportion of the population sampled, was 0.5078, 0.5560, and 0.6961, for broods of 3, 4, and 5 goslings, respectively. Thus, females hatching 5 goslings fledged 37% and 26% more goslings on

average than females hatching 3 or 4 goslings, respectively. Thus, while survival rate of individual goslings declined with increasing brood size, this reduction in survival did not completely offset the larger number of goslings produced by larger initial brood sizes. Therefore, females hatching more young (assuming equal post-fledging survival of young to reproductive age) were more fit.

The negative relationship between deviations from expected number recaptured and initial brood size implies that laying additional eggs results in diminishing returns in the number of goslings fledged per female. That is, the proportion of the initial brood that survives to fledging declines with brood size. This trend would create an upper limit to the optimal initial brood size (Rockwell, Findlay & Cooke 1987). Thus, while fitness increases with initial brood size so does the energetic cost to females, and the net gain in fitness for females laying very large clutches may be zero. This may explain the lack of 6 egg clutches in black brant (Sedinger, unpublished), whereas 6 egg clutches are common in similarly sized cackling Canada geese (Branta canadensis minima) (Mickelson 1975).

EGG SEQUENCE NUMBER

The effect of egg position in the laying sequence on gosling survival was unclear in this study. Rockwell, Findlay & Cooke (1987) suggest that lower survival of goslings from very large lesser snow goose clutches is a result of reduced survival of goslings from parasitic eggs which tend to be delayed in hatching. Kennamer, Harvey & Hepp (1990) noted that developmental asynchrony among eggs increased with increasing clutch size, and that egg hatching success declined with increasing developmental asynchrony in wood ducks (Aix sponsa). Thus, the effect of egg sequence number on gosling survival should increase with

clutch size if survival is related to asynchrony in hatching. This hypothesis is consistent with the lack of an effect of position in the laying sequence in broods of 3 and a significant result in broods of 4. Lack of an egg number relationship in broods of 5, however, is inconsistent with this hypothesis.

We hypothesize, based on the combined results of analyses of initial brood size, egg size, and egg sequence number, that the primary factors affecting gosling survival differ for goslings in different size broods. Avian predation may be concentrated on large broods (Munro & Bedard 1977; Safriel 1975) and large broods are probably more difficult for adults to protect, as evidenced by increased vigilance (Sedinger & Raveling 1990) and poorer condition of females attending larger broods (Lessells 1986). Gull predation might remove goslings from broods at random, with respect to egg size and sequence, thus making egg size and sequence effects more difficult to detect for large broods. Conversely, small broods may be less likely to experience predation, and thus mortality is more closely related to intrinsic factors such as egg size or sequence number. Under this hypothesis, lower individual survival for goslings in large broods would result from additive mortality due to both intrinsic factors (e.g. egg size) and predation.

FEMALE AGE

Young females tended to be less successful in rearing their broods than older females, however, this relationship was not significant. This is consistent with several studies that failed to show an effect of female age on brood rearing success (Afton 1984; Dow & Fredga 1984). Alternatively, both younger and less experienced females of several other species have lower total reproductive output than older females (Dow & Fredga 1984; Finney & Cooke 1978; Gauthier 1989;

Afton 1984; Forslund & Larsson 1992). This lower output may be the result of a smaller investment in the reproductive attempt (e.g. smaller clutch or egg size), or lower average nesting and brood rearing success. Young females typically lay smaller eggs than older females in brant (Flint & Sedinger 1992) and other waterfowl (Finney & Cooke 1978; Newell 1988). Young females also tend to lay smaller clutches than older females (Flint & Sedinger 1992; Gauthier 1989; Forslund & Larsson 1992; Dow & Fredga 1984; Afton 1984), and smaller initial broods fledged fewer young (this study). Additionally, young females tend to nest later than older birds (Flint & Sedinger 1992; Finney & Cooke 1978; Forslund & Larsson 1992; Afton 1984; Gauthier 1989; Dow & Fredga 1984). Forslund & Larsson (1992) used path analysis to examine factors related to lower reproductive success in young barnacle geese (Branta leucopsis) and noted that age related differences in reproductive output were associated with increased clutch size and earlier hatch dates in older birds. Therefore, the relationship between female age and brood rearing success needs to be controlled for these covariates to determine if young birds are less successful due to experience or due to their egg size, initial brood size, or hatch date. Sample size is presently insufficient to control for these variables for known age females.

EVOLUTIONARY IMPLICATIONS

Both egg size and clutch size are heritable in lesser snow geese (Lessells, Cooke & Rockwell 1989) and egg size is heritable in barnacle geese (Larsson & Forslund 1992). Given this apparent heritability and the estimated selection gradients, for both egg size and clutch size, we would expect to observe a response to selection. We have not detected a response to selection for either clutch size or egg size. However, because this population has overlapping generations, and

the age of first reproduction is >1, the response to selection will occur gradually (Rockwell, Findlay & Cooke 1987). Thus, the time span of this study may have been insufficient to detect a response to the observed selection gradients for clutch and egg size.

Alternatively, the positive association of survival to both egg size and initial brood size creates the potential for a trade-off between clutch size and egg size, in which large clutches of small eggs have the same fitness as small clutches of large eggs. Lessells, Cooke & Rockwell (1989) were unable to demonstrate a negative genetic correlation between clutch size and egg size in snow geese; however, a negative genetic correlation between these two traits exists in poultry (Jaffe 1966). Thus, one potential explanation of the lack of response of these traits to the observed selection differential, is that these two characters are negatively, genetically, correlated with each other, or some other fitness character in black brant.

Hatch date has been shown to be repeatable within individuals and has a heritable component (Findlay & Cooke 1982b; Batt & Prince 1979). This apparent heritability may be due to common environment and maternal effects (Sedinger, Flint & Lindberg, unpublished). However, under either condition, we would expect a response to the estimated selection gradient. Detection of a change in the mean of relative hatch date is not possible, thus the effect of this selection pressure should be a reduction in the variation in hatch date. The maintenance of hatch date variation under the apparent selection gradient for early hatch date is difficult to explain.

Annual environmental variation in the timing of nesting cannot explain the maintenance of hatch date variation as hatch dates, both in this study and in studies estimating heritability (Findlay & Cooke 1982b), are corrected for variation

in mean hatch dates for each year. Thus, individuals tend to hatch at a specific time relative to others, regardless of the timing of the season (Findlay & Cooke 1982b).

Hatch date is not phenotypically negatively correlated, in terms of fitness, with any other characteristics measured in our population. Indeed, clutch size declines with increasing hatch date, thus, in terms of fitness, early hatch date is positively correlated with large clutch size. The potential negative correlation between hatch date and some other fitness characteristic deserves further consideration.

In conclusion, females hatching larger initial broods, larger eggs, and hatching earlier tend to fledge more young. Individual goslings in large broods have lower survival than those in smaller broods, thus, laying additional eggs results in diminishing returns for females. Thus, gosling survival may contribute to the control of clutch size in black brant. Older females have a slight tendency to be more successful at rearing their broods. This, however, may be a result of age related differences in egg size, initial brood size, and hatch date. These variables need to be controlled for in future assessments of age related variation in brood rearing success.

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Table 1. Mean and (SE) of reproductive parameters for recaptured and not-recaptured black brant broods on the Yukon-Kuskokwim Delta, Alaska, 1987-90

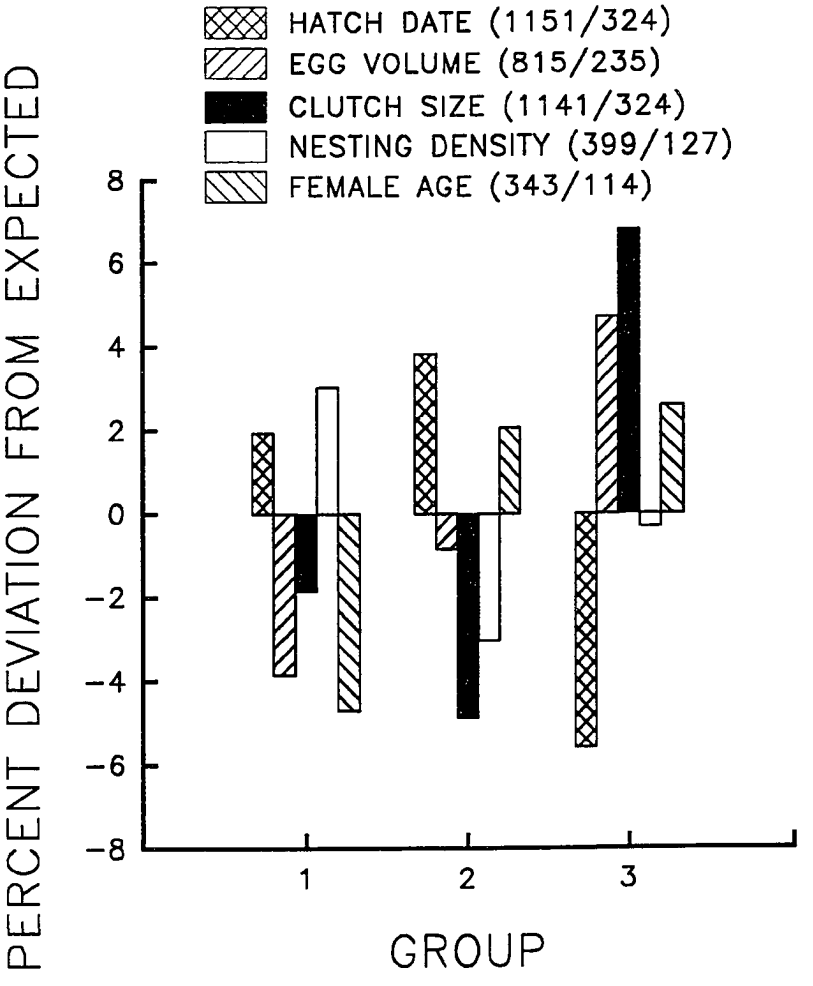
Variable	Recaptured	Not-recaptured
Hatch date (Julian)	169.8 (0.12)*	170.1 (0.08)
Clutch size	4.05 (0.07)*	3.88 (0.05)
Egg volume (ml)	82.82 (0.34)*	82.02 (0.22)
Nesting density (m)+	19.8 (0.47)	19.2 (0.78)
Female age (years)	3.76 (0.05)	3.63 (0.05)

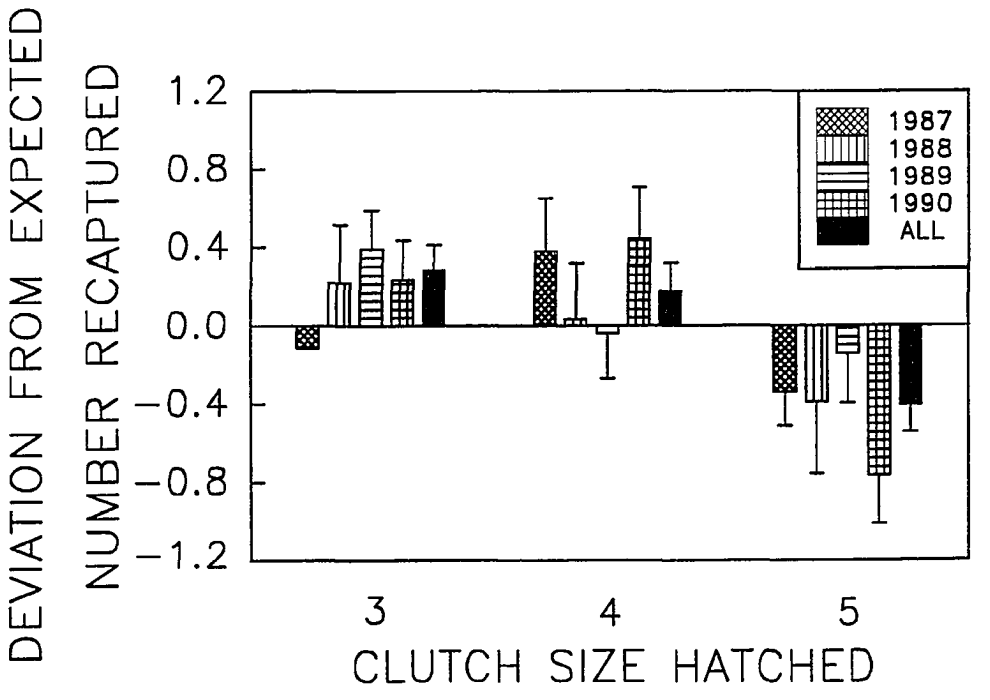
*. Recaptured significantly different than non-recaptured ($P<0.05$).
+. Average distance to 2 nearest nests.

Figure Legends

Figure 1. Deviation from expected cell value as a percentage of the recaptured sample. Cutpoints for hatch date, egg volume, and nesting density groups were set by dividing the sample size of the marked population into thirds and are presented in increasing order. Groups 1, 2, and 3, for clutch size represent clutches of 3, 4, and 5 eggs, respectively. and for female age represent 2, 3, and >3 years old, respectively. Sample sizes of the number of broods marked/recaptured are in parenthesis.

Figure 2. Mean deviation from expected number recaptured for broods hatching 3, 4, and 5 goslings. Deviation was calculated as the difference between the number of goslings recaptured and the expected number recaptured for each brood. The expected number recaptured for each brood was calculated as the product of overall proportion recaptured, from all brood sizes combined, and the initial brood size.





CONCLUSIONS

Brood rearing is an important period in the life cycle of black brant. Only about 64% of the young hatched survive to fledging and at least 20% of the successfully nesting females fledge no young in a given year. Thus, considerable individual female variation in recruitment, and thus fitness, could occur during this period.

Survival of juvenile black brant is associated with the life history characteristics of their mothers. Females hatching large broods, from large eggs, early in the season, are most successful at rearing their broods. Gosling survival within broods declines with increasing brood size, thus, hatching larger broods results in diminishing returns for females. This may be one factor contributing to ultimate regulation of clutch size in black brant.

Clutch size in arctic nesting geese has been suggested to be limited by the amount of stored nutrient reserves. The high repeatability of egg size in black brant suggests that females either cannot or do not alter their egg size annually. These two relationships predict that there should be a negative relationship between clutch size and egg size. That is, if total reserves are distributed uniformly across all egg size phenotypes, females laying small eggs should, on average, produce more eggs. Thus, we expected a negative relationship between clutch size and egg size in black brant, which we did not detect.

The positive association between both egg size and clutch size and gosling survival, creates the potential for a life-history trade-off between these two characteristics. Thus females laying large clutches of small eggs would have the same fitness as females laying small clutches of large eggs. We, however, point out that overlap in total clutch volume for clutches of different sizes suggests that

at least some fraction of the population, with comparable investments in their clutches, is engaged in these trade-offs. Both clutch size and egg size have been shown to be heritable in waterfowl. Thus, females laying large clutches of small eggs, and females laying small clutches of large eggs, within these zones of overlap, must have the same fitness. If these females did not have the same fitness, these zones of overlap in total clutch volume would not be maintained in the population. Based on this we conclude that trade offs between clutch size and egg size do occur among females in black brant.

The failure of studies, including ours, to detect the predicted negative relationship between clutch size and egg size does not invalidate the nutrient limitation hypothesis for control of clutch size in black brant as clutch size egg size trade offs still occur. However, the lack of the expected relationship suggests that the simple model of allocation of limited reserves to a clutch of eggs via a fixed eggs size must be reconsidered.